# Age and Growth of the Kiyi, Leucichthys Kiyi Koelz, in Lake Michigan

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## ABSTRACT

Ages were determined and individual growth histories were calculated from the examination and measurement of the scales of 1,649 kiyis captured at seven localities in Lake Michigan in 1931 and 1932. The numbers of individuals employed for the investigation of other phases of the life history (such as length-frequency distributions, length-weight relationship, and sex ratio) varied according to the amount of data available or required.

Age-group IV was dominant in the 1931 collections from Racine, Port Washington, and Kewaunee, Wisconsin, and age-group V dominated the 1932 samples from the Fox Islands and from three localities southward of Manistique, Michigan. A trend was noticeable toward an increase in average age from south to north. Among the explanations suggested for the observed differences in age composition were: Variation with latitude in the natural span of life; differences in fishing intensity; fluctuations in the strength of year classes (to account possibly for the shift in the dominant age group from 1931 to 1932). The oldest male kiyi belonged to the VII group and the oldest female was a member of the X group.

The possible distorting effects of such factors as gear selection traceable to differences in the mesh sizes of nets fished in 1931 and 1932, selection by nets on the basis of the condition (*K*) of the fish, and local variations in fishing intensity and hence in the selective destruction of rapidly growing individuals in the fishery were held to be sufficiently great to render doubtful the significance of most of the observed local differences in growth rate. Kiyis from all samples were combined to determine the general growth in length. The growth in weight of the Fox Islands fish, however, was considered separately as these fish were consistently lighter than kiyis of corresponding length from other localities.

The Lake Michigan kiyi grows slowly, with the females growing slightly more rapidly than the males. The grand average calculated lengths indicated, for example, that the females did not attain a total length of 10 inches until the fifth year of life or the males until the sixth. Similarly, the calculated weight of 4 ounces was not reached until the fifth or sixth year (with the actual time varying with sex and locality). The season's growth of the kiyi probably begins sometime in May and most or all of the growth is completed by the end of August.

The calculated lengths of the age groups exhibited large discrepancies that differed from "Lee's phenomenon" as ordinarily observed in that the data for the later rather than the earlier years of life were affected most severely. Chief among the factors held responsible for these discrepancies were gear selection and the selective destruction of the more rapidly growing individuals in the fishery. Errors inherent in the (direct-proportion) method of computing growth from scale measurements were considered to have been unimportant. The Lake Michigan kiyi exhibits growth compensation—the tendency for the smaller of the young fish to have the more rapid growth in the later years of life.

Comparisons with the average lengths and weights of the age groups of the Lake Ontario kiyi given by Pritchard (1931) indicated the Lake Michigan fish to be the larger at the earlier ages (age-groups II and III) and the smaller at the later ages (age-groups IV to VI).

The length-frequency distributions of the age groups exhibited extensive overlap. As many as eight age groups were represented in a single centimeter interval of length. The length frequencies and average lengths of all fish collected, arranged according to the mesh sizes of the gill nets by which they were captured, revealed that the selective action of these nets in the taking of kiyis was much more obvious in the numbers of fish in the catch than in

their average size. As an illustration, in 1930-1931, the 2¾-inch-mesh nets took fish that were only 0.1 inch longer than those in 2½-inch meshes but captured less than one fourth as many. Gill nets fished in northern Lake Michigan in 1932 captured kiyis that averaged 0.2 to 0.4 inch longer than those taken in the same meshes in southern Lake Michigan in 1930-1931.

Because of the more slender form of kiyis from the northeastern island region of Lake Michigan, data on the general length weight relationship were compiled separately for fish of that area and for those of the great central basins of the lake. In both regions the weight increased to a power slightly greater than the cube of the length. Available information on condition indicated that the coefficient ($K$) was higher in August and early September than in May, June, and July. Condition declined from early September to October and early November—the latter period the time of most active spawning. Spawning itself was accompanied by an additional loss of about 12 per cent of the body weight of females and of somewhat less than 2 per cent of the weight of males. Analysis of the variations of $K$ within a group that was homogeneous with respect to age, sex, maturity, and time of collection revealed that a net of a particular mesh size tends to take the heavier of the shorter fish and the lighter of the longer fish within its range of effectiveness. Among fish of the same length the values of $K$ tended to increase with increase in the mesh size of the nets employed for their capture.

Practically all fish in the samples were mature (only 11 immature in more than 6,000). These "immature" fish were probably "non-functional" since all of them approached or exceeded the average length of the mature kiyis.

Females were strongly predominant in the collections at all seasons but were relatively more plentiful during the summer (90 per cent of the total) than during the spawning period (75 per cent). Possible factors contributing to this predominance of females and to the change in the sex ratio at the spawning season were discussed. A decrease in the relative abundance of males with increase in age appears to be characteristic of the kiyi. This decrease indicates a differential mortality of th sexes (greater relative destruction of males in the spawning period when they are unusually abundant or a greater natural mortality rate for the males).

Current fishery regulations on mesh size and closed seasons afford the kiyi good protection but offer no guarantee against depletion from too intensive fishing.

## INTRODUCTION

Except for the bloater, *L. hoyi*, the kiyi, *Leucichthys kiyi*, is the smallest of the seven known Great Lake species of chubs. In Lake Michigan, kiyis are generally abundant throughout the great central basins at depths of 40 or 50 fathoms down to at least 90 fathoms and are also taken frequently, albeit in small numbers, in shallower water. They are scarce, however, in the island region of northeastern Lake Michigan and have never been reported from Green Bay.

Because of its small size the kiyi was probably of little or no importance in the early commercial fishery of Lake Michigan. As the abundance of the larger, more valuable chubs declined, however, fishermen were forced to reduce the mesh size of their nets in order to take the smaller varieties. With this change of gear the kiyi entered the commercial catch and today makes up a substantial portion of the take

in some localities. The growing importance of the kiyi makes it desirable to have information on such phases of its natural history as distribution, size, age, growth, length-weight relationship, sex ratio, maturity, and spawning.

The kiyi was described originally from Lake Michigan (Koelz, 1921). A typical *kiyi* occurs also in Lake Superior and Lake Huron. The Ontario form, however, has been assigned to the subspecies *orientalis* (Koelz, 1929). Kiyis are absent from Lake Erie, which contains no chubs.

The one previous study of the growth of the species was made for the Lake Ontario kiyi by Pritchard (1931). For the Lake Michigan form the available published information has been limited to that contained in the two papers by Koelz, mentioned in the preceding paragraph. Koelz' 1929 publication included in addition to taxonomic data certain observations on the distribution, abundance, and breeding habits of the species. A rather comprehensive study by Hile and Deason (1947) of the bathymetric and geographical distrbiution, regional abundance, and spawning season and grounds of the Lake Michigan kiyi appears in the same volume with the present publication.

We wish to thank Dr. John Van Oosten, In Charge of Great Lakes Fishery Investigations, Fish and Wildlife Service, for his critical examination of the original manuscript and his excellent suggestions for its improvement. Dr. Frank W. Jobes of the Great Lakes Staff kindly prepared the three figures appearing in this paper.

## MATERIALS AND METHODS

Determinations of age and calculations of individual growth histories from the examination and measurement of scales were made for 1,649 kiyis collected by means of experimental chub gill nets[1] at seven localities and on eight dates (Table 1). The two samples from Port Washington have been treated in all analyses as a single collection. The fish taken out of Charlevoix will be designated the Fox Islands collection in later pages. The numbers of specimens used for certain other phases of the investigation were: Sex ratio—7,028; length-frequency distributions—6,625; relationship between total length and standard length—6,017; length-weight relationship—4,696.

All measurements and weights were taken in the field from fresh specimens. Measurements of length (total lengths were measured to the tip of the tail with the upper and lower edges parallel and standard lengths to the base of the caudal peduncle), which were recorded to the nearest millimeter, were made with a steel tape held as nearly parallel as possible to the long axis of the body. Lengths and incre-

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[1]The experimental chub nets fished in Lake Michigan included the following mesh sizes (extension measure in inches as manufactured) in each standard gang: 1930 and 1931— 2⅜, 2½, 2⅝, 2¾, and 3; 1932—2½, 2⅝, and 2¾. See Deason (1932), Van Oosten (1933), and Hile and Deason (1947) for certain particulars relative to the participating organizations and the purposes and conduct of this experimental fishing.

ments of length presented in this paper in inches are total; those given
in millimeters are standard. Weights were recorded to the nearest
tenth (1931) or quarter (1930 and 1932) of an ounce.

TABLE 1.—*Location and date of capture of 1,649 Lake Michigan kiyis for which
determinations of age and calculations of growth histories were made*

| Port | Date | Course | Distance (miles) | Number of fish |
|------|------|--------|------------------|----------------|
| Manistique, Mich. ...................... | June 14, 1932 | SxW3/16W | 30¾ | 202 |
| Do. ....................................... | July 9, 1932 | SExE1/4E | 21 | 125 |
| Do. ....................................... | Sept. 7, 1932 | SSE5/16E | 14¾ | 194 |
| Cha levoix, Mich.[1] ...................... | Aug. 13, 1932 | W1/8S | 35 | 64 |
| Kewaunee, Wis. ...................... | Oct. 15, 1931 | ExS1/4S | 11 | 313 |
| Po·t Washington, Wis. ........... | Aug. 13, 1931 | ExN1/8N | 16 | 495 |
| Do. ....................................... | Aug. 21, 1931 | | | |
| Ra·ine, Wis. ........................... | Oct. 9, 1931 | ExN1/2N | 22½ | 256 |

[1]Near the Fox Islands.

Scales for age and growth determinations were mounted on glass
slides and examined by means of a microprojection apparatus at the
magnification X 40.7. The diameters of the entire scale and of the
growth field within each annulus were measured to the nearest milli-
meter. Computations of growth from scale measurements were made
by direct proportion, that is, on the assumption that the ratio of body
length to scale diameter is constant from the time of the formation of
the first annulus. Although no data are available on the body-scale
relationship of the kiyi, this method of calculation was proved to be
satisfactory for the related species, *L. artedi* (Van Oosten, 1929).

Ages have been designated by roman numerals corresponding to the
number of annuli or year marks on the scales. The term mature as
employed here refers to fish that would have spawned at the next
season, regardless of whether or not they had spawned previously.

## AGE COMPOSITION

In the compilation of the data on the age composition of the sam-
ples of kiyi (Table 2) the sexes were combined for each locality, and
the three 1932 collections from Manistique were treated as one. Males
were generally so scarc (only 10.4 per cent of the grand total) that a
separate presentation of the detailed data for the sexes in each collec-
tion did not seem to be justified. At the bottom of the table, however,
has been given the age composition of males and females for all col-
lections combined. The Manistique samples were combined because of
the relatively small variations in the age composition from date to
date.[2]

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[2]The numerical representation of the fish of each sex in each age group of the various
samples (including each of the individual Manistique collections) will be found in Tables
3 and 4. Questions concerning the relative abundance of males and females are considered
in the section dealing with sex ratio.

TABLE 2.—*Numerical and percentage (in parentheses) representation of the age groups of kiyis from different localities in Lake Michigan and for all localities combined*

| Locality | Age group | | | | | | | | Total and average[1] |
|---|---|---|---|---|---|---|---|---|---|
| | II | III | IV | V | VI | VII | VIII | X | |
| Manistique ........ | 2 (0.4) | 14 (2.7) | 68 (13.0) | 246 (47.2) | 149 (28.6) | 37 (7.1) | 4 (0.8) | 1 (0.2) | 521 5.26 |
| Fox Islands ...... | .... .... | 2 (3.1) | 17 (26.6) | 29 (45.3) | 12 (18.8) | 4 (6.2) | .... .... | .... .... | 64 4.98 |
| Kewaunee ........ | 4 (1.3) | 68 (21.8) | 150 (47.9) | 75 (23.9) | 15 (4.8) | .... .... | 1 (0.3) | .... .... | 313 4.11 |
| Port Washington | 1 (0.2) | 33 (6.7) | 290 (58.6) | 147 (29.7) | 21 (4.2) | 2 (0.4) | 1 (0.2) | .... .... | 495 4.33 |
| Racine .............. | 26 (10.2) | 74 (28.9) | 115 (44.9) | 33 (12.9) | 6 (2.3) | 2 (0.8) | .... | .... | 256 3.71 |
| All localities Male .............. | 7 (4.0) | 37 (21.5) | 71 (41.3) | 44 (25.6) | 11 (6.4) | 2 (1.2) | .... .... | .... .... | 172 4.12 |
| Female .......... | 26 (1.8) | 154 (10.4) | 569 (38.5) | 486 (32.5) | 192 (13.0) | 43 (2.9) | 6 (0.4) | 1 (0.1) | 1,477 4.56 |
| Both .............. | 33 (2.0) | 191 (11.6) | 640 (38.8) | 530 (32.1) | 203 (12.3) | 45 (2.7) | 6 (0.4) | 1 (0.1) | 1,649 4.51 |

[1]The second figure for each port or sex is the average number of annuli.

The outstanding feature of the data of Table 2 is the trend toward an increase in the average age of kiyis from south to north. The only exception to this trend was provided by the Kewaunee fish which averaged slightly younger than did those from Port Washington. At Racine, age-group IV was dominant (44.9 per cent) with age-group III second in abundance (28.9 per cent). The IV group was dominant at Port Washington (58.6 per cent) and Kewaunee (47.9 per cent) also. At both of these ports, however, V-group kiyis were more plentiful than were III-group fish. The dominance shifted to the V group in the Fox Islands sample (45.3 per cent) with age-group IV the next strongest. Finally, off Manistique age-group V was dominant (47.2 per cent) with the VI group second. These local differences in age composition resulted in a range in the average age from 3.71 at Racine to 5.26 at Manistique.

Age-group IV was dominant (38.8 per cent) in the combined collections. The V group was only slightly less abundant (32.1 per cent) and was between two and three times as well represented as either age-group VI (12.3 per cent) or age-group III (11.6 per cent). Other groups were represented only sparsely (0.1 to 2.7 per cent). The comparison of the data for the sexes reveals that the younger age groups (II to IV) were relatively better represented while the older age groups (V and older) were more poorly represented among the males than among the females. The average ages of the sexes were: Males—4.12; females—4.56.

Some of the local differences in age composition and average age are sufficiently large to be taken as indicative of real differences among the samples. The possible effects of certain distorting factors must be considered, however, before these variations can be discussed in terms of real differences among the kiyi stocks of the several regions.

A possible major source of distortion lay in the change of gear from nets of five mesh sizes in 1930 and 1931 (no scale collections in the former year) to nets of three mesh sizes in 1932 (see footnote 1). The omission of the 2⅜ mesh in 1932 (the year of collection of the Fox Islands and Manistique samples) could have been extremely damaging since nets of that mesh size were the most successful of the five employed in earlier years for the capture of kiyis (Table 6). In order to estimate the effects of the change in gear, the average ages were determined of the kiyis taken off Racine, Port Washington, and Kewaunee in nets of the same three mesh sizes that were fished in 1932 (that is, the samples from the 2⅜- and 3-inch-mesh nets were excluded). Comparisons of the average ages of fish from nets of five and of three mesh sizes appear below (numbers of fish in parentheses) :

| Port | *Average age of kiyis* | |
|------|------------------------|--------------------------|
|      | *From five mesh sizes* | *From three mesh sizes* |
| Kewaunee | 4.11 | 4.36 |
|          | (313) | (196) |
| Port Washington | 4.33 | 4.43 |
|                 | (495) | (275) |
| Racine | 3.71 | 3.40 |
|        | (256) | (144) |

The ages of kiyis from nets of the three mesh sizes averaged slightly higher than did those of fish from nets of five mesh sizes in both the Kewaunee and Port Washington samples. At Racine, however, the kiyis from three nets averaged somewhat younger than did those from five. Because the differences between the average ages of fish from the two groups of nets were not large or consistent as to direction, it may be concluded that the change in gear from 1931 to 1932 is not a distorting factor in the observed differences in age composition and average age of the fish taken in the two years.

Since males usually averaged younger than females of the same collection, and since the Kewaunee and Racine samples were taken during the spawning period, at which time males ordinarily are relatively more plentiful than in other seasons (p. 133), the possible effects of the greater relative abundance of males in these two collections on the determination of the average age was investigated. Computations revealed that had the percentages of males and females in the Kewaunee collection been the same as in the August samples from

Port Washington the average age of the Kawaunee fish (sexes combined) would have been 4.13 rather than 4.11. In the Racine samples where the average age of the males, contrary to the usual situation, was greater than that of the females, a similar reduction in the representation of the males would have reduced the average for the combined sexes from 3.71 to 3.69. It was impossible to demonstrate, therefore, that the greater abundance of males in the spawning-run samples affected significantly the average age.

Local differences in growth rate in combination with the selection of fish according to size by the gill nets offer a third possible source of distortion. As a gill net of a particular mesh tends to take fish over a relatively limited range of size, the individuals from slowly growing stocks might be expected to average older than those from populations with rapid growth. It will be brought out in the next section, however, that aside from the tendency of kiyis of northeastern Lake Michigan to be lighter (but not shorter) than fish of corresponding age from other localities the local variations in the growth of the Lake Michigan kiyi were small. The fish of the Fox Islands sample possibly might have had a slightly lower average age had they been less slender. There is no other evidence for local differences in growth rate that could be expected to affect the age composition of the samples.

Since the apparently most probable sources of bias were demonstrated to have had no important effect on the data of Table 2, it may be concluded that the observed local variations in age composition represented, in the main, real differences among the populations from which the samples were drawn.

It is possible that a progressive south-to-north increase in the natural life span of the kiyi may have contributed to the local fluctuations in age composition. It is conceivable also that differences between the average ages in 1931 (Racine, Port Washington, and Kewaunee collections) and in 1932 (Fox Islands and Manistique collections) were in part the result of an exceptionally strong 1927 year class that was dominant as the IV group in 1931 and as the V group in 1932. On the other hand, some of the variation—notably the differences between the northern (State of Michigan) and southern (State of Wisconsin) samples—can be explained logically as the result of differences in the intensity of the fishery and consequently in the mortality rate.

Although information on the amount of gear lifted is lacking for Wisconsin waters previous to 1936[3] and hence no exact comparison can be made with Michigan data, it is well known that at the time of the chub-net investigations the fishery for chubs was far more intensive in the Wisconsin waters than in the Michigan waters of Lake Michigan. The inequality in fishing pressure was doubtless much greater for the kiyi in particular than for chubs in general, because of dif-

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[3] Records of the amount of all types of gear lifted, beginning with 1929, are available in the files of the Great Lakes laboratory of the Fish and Wildlife Service for the State of Michigan waters of the Great Lakes.

ferences in the mesh size of commercial shub nets in the two states. For some time before and during the years of the experimental fishing the minimum legal mesh size for chub nets in the State of Michigan waters was $2\frac{3}{4}$ inches (extension measure). This regulation was reasonably well enforced. In Wisconsin the minimum legal mesh size for chub nets was $2\frac{5}{8}$ inches, but so many fishermen used a smaller mesh that the true average difference between the meshes in Michigan and Wisconsin waters was without doubt substantially greater than the indicated one-eighth inch. Since the kiyi is a small, slowly growing chub the nets of Wisconsin fishermen must have been much more effective for its capture than were the larger-meshed nets of the Michigan operators.

At first thought, the suggestion that the higher average age of kiyi from northern Lake Michigan was the result of a lower fishing intensity would appear to conflict with the statement by Hile and Deason (1947) to the effect that Wisconsin and Michigan fishermen probably exploit the same stocks of the species. That statement referred, however, to southern Lake Michigan waters (near and south of the Kewaunee-Frankfort line). The more northerly grounds from which the Manistique and Fox Islands samples were collected were rather remote from the chief centers of the Wisconsin fishery and therefore these kiyis may have been drawn from stocks that were subject to little or no exploitation by Wisconsin operators. It is known also that in the State of Michigan waters the intensity of the chub fishery in the northerly region was generally less than toward the south. Furthermore, the intensity of the chub fishery of the Manistique and northeastern areas in both 1931 and 1932 (1930 also off Manistique) was below the 1929-1943 average.[4] The combined effects of larger mesh in Michigan chub nets and the low fishing intensity in northern Lake Michigan may have permitted the kiyis of that region to survive to a greater average age than did the fish of more southerly waters.

The data given by Hile and Deason (1947) on the abundance of kiyis yielded no evidence for an accumulated stock in the northern waters, since the abundance was apparently about the same in the Manistique region as in southern Lake Michigan, and kiyis were scarce at localities in the northeastern island region. It should be remembered, however, that general ecological conditions doubtless vary in these widely separated regions, and hence that with respect to the natural carrying capacity, a population density that is sparse for one area may represent an accumulated stock for another.

### LENGTH AND WEIGHT AT CAPTURE; LENGTH-FREQUENCY DISTRIBUTIONS

Some of the variations in the average length and weight of kiyis of corresponding age and sex of the different collections (Tables 3 and 4) doubtless represent true differences among the samples. The extent to

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[4] This statement is based on records of the actual quantity of gear lifted.

which these variations indicate real differences in the normal growth rate of kiyis in the several regions of the lake, however, is difficult to decide. Comparisons of the average size of the fish in the corresponding age groups in different collections should include consideration of certain sources of variability not related at all to the true rate of growth.

It may be pointed out first that comparisons of length are more reliable than comparisons of weight. Seasonal and annual fluctuations in condition are sufficiently great (p. 122) to bring about rather large variations in average weight that are independent of length.[5]

The time of capture during the growing season doubtless affected some of the averages of Tables 3 and 4. In the Manistique collections the size of the female kiyis (males were extremely scarce in these samples) of every age group increased from June 14 to July 9. The averages for the September collection indicated some increase in weight after July but did not show an increase in length (increase in one age group; decrease in two age groups; no change in two age groups).[6] The Fox Islands and Port Washington averages also might have been slightly greater had the collections been made later in the season, although the data of a later section (p. 120) suggest that the increase in size after mid-August probably would not have been large.

The effects of gill-net selection also should be considered in the comparison of the average size of the fish. Cognizance should be taken particularly of the fact that gill nets of a greater range of mesh size (five sizes) were employed in 1931 than in 1932 (three sizes). In order to estimate the probable effects of this change in gear the average lengths and weights of the three best represented age groups (III, IV, and V) of female kiyis in the three 1931 collections were determined with the samples from the 2⅜- and 3-inch-mesh nets excluded. Of the nine age groups involved, two showed no increase in length over the average for fish from five nets, four showed an increase of 0.1 inch, and three an increase of 0.2 inch. All nine age groups exhibited an increase in average weight ranging from 0.05 to 0.43 ounce and averaging 0.27 ounce. It appears, then, that the age groups of the 1931 collections would have averaged slightly larger had the same gear been used in that year as in 1932. Conversely, it would be expected that the age groups of the Manistique and Fox Islands collections would have had somewhat lower average lengths and weights had nets of five rather than three mesh sizes been employed for their capture.

Even without change of gear, gill-net selection can be of importance since variations in condition or relative heaviness can affect the

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[6]The weights of the kiyis of the Fox Islands collection require special consideration (p. 124).
[6]It will be shown later f om the calculated increments of length for the 1932 season that a certain amount of growth in length did occur after July 9, but that this growth was obscured in the comparisons of the ave age sizes at capture in July and September by the fact that the sample of the latter month was made up of fish that had made slower past growth than had the kiyis of the July collection (p. 118).

TABLE 3.—*Average total length (inches) and weight (ounces) of male kiyis of each age group in the various collections from Lake Michigan*

[The averages at the bottom of the table include also the standard lengths in millimeters and the weights in grams]

| Locality and date | Item | Age group | | | | | | Average or total |
|---|---|---|---|---|---|---|---|---|
| | | II | III | IV | V | VI | VII | |
| Manistique (June 14, 1932) | Total length.... | 7.0 | ...... | 10.5 | 9.8 | 9.8 | 11.2 | 9.9 |
| | Weight ......... | 1.50 | ...... | 5.00 | 4.00 | 4.00 | 6.50 | 4.31 |
| | Number of fish | 1 | ...... | 4 | 6 | 1 | 1 | 13 |
| Manistique (July 9, 1932) | Total length.... | ...... | ...... | 8.9 | 11.3 | 10.2 | ..... | 10.2 |
| | Weight ......... | ...... | ...... | 3.25 | 6.25 | 4.38 | ..... | 4.56 |
| | Number of fish | ...... | ...... | 1 | 1 | 2 | ..... | 4 |
| Manistique (Sept. 7, 1932) | Total length.... | ...... | ...... | 10.6 | 10.8 | 10.4 | ..... | 10.6 |
| | Weight ......... | ...... | ...... | 6.00 | 6.15 | 5.50 | ..... | 5.92 |
| | Number of fish | ...... | ...... | 1 | 5 | 3 | ..... | 9 |
| Fox Islands (Aug. 13, 1932) | Total length.... | ...... | 7.6 | 9.8 | 10.2 | 10.3 | ..... | 9.8 |
| | Weight ......... | ...... | 2.00 | 4.00 | 4.50 | 4.62 | ..... | 4.09 |
| | Number of fish | ...... | 1 | 2 | 3 | 2 | ..... | 8 |
| Kewaunee (Oct. 15, 1931) | Total length.... | 8.9 | 9.7 | 10.1 | 10.1 | 10.9 | ..... | 9.9 |
| | Weight ......... | 3.40 | 4.30 | 4.60 | 4.91 | 6.20 | ..... | 4.57 |
| | Number of fish | 1 | 19 | 20 | 12 | 1 | ..... | 53 |
| Port Washington (Aug. 13 and 21, 1931) | Total length.... | 9.7 | 9.2 | 9.9 | 10.3 | 11.5 | ..... | 9.9 |
| | Weight ......... | 4.20 | 3.73 | 4.90 | 5.20 | 7.90 | ..... | 4.85 |
| | Number of fish | 1 | 6 | 23 | 9 | 1 | ..... | 40 |
| Racine (Oct. 9, 1931) | Total length.... | 10.2 | 10.4 | 10.5 | 10.6 | 10.3 | 10.1 | 10.5 |
| | Weight ......... | 4.70 | 5.19 | 5.00 | 5.02 | 4.60 | 5.50 | 5.03 |
| | Number of fish | 4 | 11 | 20 | 8 | 1 | 1 | 45 |
| All collections except from Manistique in June and from the Fox Islands | Total length.... | 9.9 | 9.8 | 10.1 | 10.4 | 10.5 | 10.1 | 10.1 |
| | Weight ......... | 4.40 | 4.48 | 4.83 | 5.23 | 5.50 | 5.50 | 4.86 |
| | Standard length | 208 | 205 | 214 | 218 | 223 | 211 | 213 |
| | Weight (grams) | 125 | 127 | 137 | 148 | 156 | 156 | 138 |
| | Number of fish | 6 | 36 | 65 | 35 | 8 | 1 | 151 |

TABLE 4.—*Average total length (inches) and weight (ounces) of the female kiyis of each age group in the various collections from Lake Michigan*

[The averages at the bottom of the table include also the standard lengths in millimeters and the weights in grams]

| Locality and date | Item | \|\| II | III | IV | V | VI | VII | VIII | X | Average or total |
|---|---|---|---|---|---|---|---|---|---|---|
| Manistique (June 14, 1932) | Total length | ..... | 9.3 | 10.2 | 10.7 | 10.9 | 11.0 | 10.8 | ..... | 10.7 |
| | Weight | ..... | 3.60 | 4.74 | 5.56 | 6.04 | 6.00 | 6.00 | ..... | 5.57 |
| | Number of fish | ..... | 5 | 23 | 98 | 54 | 8 | 1 | ..... | 189 |
| Manistique (July 9, 1932) | Total length | 10.0 | 10.0 | 10.5 | 10.9 | 11.1 | 11.1 | ..... | ..... | 10.9 |
| | Weight | 4.30 | 4.68 | 5.01 | 5.94 | 6.20 | 6.03 | ..... | ..... | 5.79 |
| | Number of fish | 1 | 7 | 19 | 47 | 32 | 15 | ..... | ..... | 121 |
| Manistique (Sept. 7, 1932) | Total length | ..... | 10.8 | 10.5 | 10.6 | 11.0 | 11.1 | 11.4 | 10.6 | 10.8 |
| | Weight | ..... | 5.75 | 5.91 | 5.96 | 6.58 | 6.85 | 7.58 | 5.75 | 6.23 |
| | Number of fish | ..... | 2 | 20 | 89 | 57 | 13 | 3 | 1 | 185 |
| Fox Islands (Aug. 13, 1932) | Total length | ..... | 9.9 | 10.6 | 10.9 | 11.1 | 11.3 | ..... | ..... | 10.9 |
| | Weight | ..... | 2.75 | 4.82 | 5.60 | 5.80 | 5.69 | ..... | ..... | 5.38 |
| | Number of fish | ..... | 1 | 15 | 26 | 10 | 4 | ..... | ..... | 56 |
| Kewaunee (Oct. 15, 1931) | Total length | 9.7 | 9.8 | 10.3 | 10.7 | 10.7 | ..... | 10.6 | ..... | 10.3 |
| | Weight | 4.58 | 4.47 | 5.33 | 5.78 | 6.32 | ..... | 5.75 | ..... | 5.32 |
| | Number of fish | 3 | 49 | 130 | 63 | 14 | ..... | 1 | ..... | 260 |
| Port Washington (Aug. 13 and 21, 1931) | Total length | ..... | 9.8 | 10.3 | 10.7 | 10.8 | 11.5 | 12.4 | ..... | 10.4 |
| | Weight | ..... | 4.80 | 5.42 | 5.97 | 6.17 | 7.10 | 8.75 | ..... | 5.60 |
| | Number of fish | ..... | 27 | 267 | 138 | 20 | 2 | 1 | ..... | 455 |
| Racine (Oct. 9, 1931) | Total length | 10.2 | 10.5 | 10.9 | 10.9 | 10.5 | 11.9 | ..... | ..... | 10.7 |
| | Weight | 5.11 | 5.68 | 5.99 | 6.05 | 5.20 | 7.40 | ..... | ..... | 5.80 |
| | Number of fish | 22 | 63 | 95 | 25 | 5 | 1 | ..... | ..... | 211 |
| All collections except from Manistique in June and from the Fox Islands | Total length | 10.1 | 10.1 | 10.4 | 10.7 | 10.9 | 11.2 | 11.4 | 10.6 | 10.5 |
| | Weight | 5.03 | 5.07 | 5.50 | 5.94 | 6.34 | 6.49 | 7.45 | 5.75 | 5.69 |
| | Standard length | 213 | 212 | 218 | 225 | 230 | 234 | 241 | 228 | 221 |
| | Weight (grams) | 143 | 144 | 156 | 168 | 180 | 184 | 211 | 163 | 161 |
| | Number of fish | 26 | 148 | 531 | 362 | 128 | 31 | 5 | 1 | 1,232 |

average length of the fish captured. Selection on this basis is believed, for example, to account for the fact that the best represented age groups (IV to VII) of the females of the Manistique collection of September had average lengths that were the same or less than those of fish of the same ages in the July collection. The weight of the fish increased in every age group, and the calculated increments (p. 118) indicated that growth in length did take place after July 9. The gill nets simply took the shorter of the relatively plump September fish. The average lengths of the kiyis of other age groups doubtless were affected by the condition of the fish on the grounds at the time of capture. (See pp. 128-133 for data and discussion on the effect of gill-net selection on the estimation of the average value of the coefficient of condition.)

The selective destruction of the more rapidly growing individuals in the fishery offers another important source of differences in the average size of fish of the same age in the various samples. The more intensive the fishery the more likely are the individuals with rapid growth to be captured at an early age. Samples drawn from the residual stock of slow growers will yield averages that are too low in comparison with the true growth rate. The effects of this selection will vary, of course, with local variations in fishing pressure. The destruction of the rapidly growing individuals in the fishery very probably contributed to the low average size of the kiyis of the Kewaunee and Port Washington samples since the exploitation of shubs is known to have been particularly heavy in those regions of Lake Michigan.

The sources of selection and of distortion of the data just outlined seem to be adequate to explain most of the variations in the average lengths and weights of the age groups in the different collections. Although some real local differences in growth rate may exist, it is believed that the only demonstrable regional difference is provided by the growth in weight of the kiyis of the Fox Islands collection, in which the average weights of the age groups were rather consistently low. The weight of the IV-group females, for example, was less in the Fox Islands sample than in any other collection except the one taken off Manistique on June 14, and these Manistique fish averaged the shorter by 0.4 inch. Furthermore, the average weight of the Fox Islands IV group was less than that of four other samples of IV-group females with lower average lengths. A similar situation held for the other age groups of the Fox Islands kivis. The slow growth in weight of the Fox Islands fish is the result of differences between the length-weight relationships of kiyis from the island region of northeastern Lake Michigan and from the central basins of the lake (p. 124). Growth in length was much the same at the Fox Islands as elsewhere in Lake Michigan.

˙ If the June 14 sample from Manistique is excluded because of its collection early in the growing season and the Fox Islands fish are omitted because of the slow growth in weight, the data for the re-

maining collections may be combined to obtain an estimate of the general relationship between the age and size of kiyis captured late in the growing season (see bottoms of Tables 3 and 4). Attention may be given first to the data for the females since fish of that sex formed the bulk of the collections.

The differences among the average lengths and weights of the age groups of female kiyis were in general small. Although an increase in both length and weight did occur in every age group from IV to VIII, the length increments were only 0.2 or 0.3 inch (4 to 7 millimeters) and the weight increments were only 0.15 to 0.96 ounce (4 to 27 grams). Age-groups III and X provided exceptions to the increase in size with increase in age. The almost identical averages for age-groups II and III can be considered the result of gill-net selection; the scarcity of II-group fish indicates that only the larger members of the age group were captured. (The fact that III-group females were much less numerous than IV-group females suggests that the averages for the III group also may have been too high.) No significance can be attached to the low figures of length and weight of age-group X since that age was represented by only one fish.

The grand average length of all females (exclusive of the Manistique collection in June and the Fox Islands collection) was 10.5 inches (221 millimeters) and the grand average weight was 5.69 ounces (161 grams).

The data for the males resembled those for the females in that age-groups II and III exhibited only small differences, and the averages for the later age groups showed a slow but steady increase in length and weight with the exception of the oldest age group (VII) which was represented by only one individual. The length increments of the age groups that showed an increase in size ranged from 10.1 to 0.3 inch (4 to 9 millimeters) and the weight increments from 0.27 to 0.40 ounce (8 to 11 grams).

Females averaged longer and heavier than males of the same age. In the best represented age groups the length advantage of the females was 0.3 inch (age-groups III, IV, and V) or 0.4 inch (age-group VI). The weight advantage of the females increased regularly from 0.59 ounce in the III group to 0.84 ounce in the VI group. For all age groups combined the average length of the males was 0.1 inches (0.4 inch less than the average for the females) or 213 millimeters. The grand average weight was 4.86 ounces (0.83 ounce less than the average for the females) or 138 grams.

The small differences among the average sizes of the fish of the several age groups are brought out forcibly by the length-frequency distributions of kiyis of the late-season collections[7] (Table 5). It is true that in age-groups IV to VIII the increases in the average length

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[7]The Fox Islands collection, which was excluded in the computation of the averages at the bottom of Tables 3 and 4 because of the low average weights of the age groups, was employed in the preparation of the length-frequency tabulations since apparently the growth in length in the Fox Islands region was similar to that in other areas.

TABLE 5.—*Length frequencies of the age groups of kiyis, with the data combined for all collections, except the June collection from Manistique*

[The total lengths in the second column are equivalent to the midpoints of the intervals of standard length.  M = male;  F = female]

| Standard length, millimeters | Total length, inches | II M | II F | III M | III F | IV M | IV F | V M | V F | VI M | VI F | VII M | VII F | VIII F | X F | Totals M | Totals F | Grand total | Percentage |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 150-159 | 7.4 | | | 1 | | | | | | | | | | | | 1 | | 1 | 0.1 |
| 170-179 | 8.3 | | | | | | 1 | | 1 | | | | | | | | 1 | 1 | 0.1 |
| 180-189 | 8.8 | 2 | | | | | 1 | | 1 | | | | | | | 3 | 3 | 6 | 0.4 |
| 190-199 | 9.3 | 2 | 2 | 2 | 1 | 1 | 1 | | 2 | 1 | | | | | | 18 | 32 | 50 | 3.4 |
| 200-209 | 9.8 | 1 | 6 | 7 | 17 | 5 | 10 | 3 | 17 | 2 | 6 | | 1 | | | 42 | 166 | 208 | 14.4 |
| 210-219 | 10.3 | | 11 | 13 | 49 | 16 | 88 | 9 | 79 | 3 | 16 | | 4 | 1 | | 51 | 355 | 406 | 28.0 |
| 220-229 | 10.7 | | 7 | 8 | 37 | 29 | 208 | 12 | 156 | 3 | 41 | 1 | 7 | 2 | | 29 | 404 | 433 | 29.9 |
| 230-239 | 11.1 | | | 6 | 34 | 14 | 157 | 5 | 107 | 3 | 46 | | 6 | | 1 | 11 | 220 | 231 | 16.0 |
| 240-249 | 11.6 | | | | 5 | 2 | 54 | 6 | 21 | 1 | 22 | | 14 | 1 | | 3 | 88 | 91 | 6.3 |
| 250-259 | 12.1 | | | | 1 | | 26 | 2 | 5 | | 7 | | 3 | 1 | | 1 | 18 | 19 | 1.3 |
| 260-269 | 12.6 | | | | | | 1 | 1 | | | | | | | | | 1 | 1 | 0.1 |
| Total | | 6 | 26 | 37 | 149 | 67 | 546 | 38 | 388 | 10 | 138 | 1 | 35 | 5 | 1 | 159 | 1,288 | 1,447 | ...... |
| Aver. total length | | 9.9 | 10.1 | 9.7 | 10.1 | 10.1 | 10.4 | 10.4 | 10.7 | 10.5 | 10.9 | 10.1 | 11.2 | 11.4 | 10.6 | 10.1 | 10.5 | 10.5 | ...... |
| Aver. stand. length | | 208 | 213 | 204 | 212 | 214 | 218 | 218 | 225 | 222 | 230 | 211 | 234 | 241 | 228 | 213 | 221 | 220 | ...... |

of the females were accompanied by 1-centimeter increases in the modal length. (Among the weakly represented males the position of the mode varied irregularly.) Nevertheless, the overlap of the frequency distributions of the age groups was generally so great that the length of kiyis must be considered a very poor index of the age. Especialy striking is the situation at 220-229 millimeters at which interval were represented all of the eight age groups of females and five of the six age groups of males present in the samples. Similar though less extreme overlapping of age groups occurred at other length intervals in which fish were abundant.

The distribution for the combined age groups were remarkably compact in spite of the fact that gill nets of three or five mesh sizes were used for the collection of the samples. One hundred twenty-two or 76.7 per cent of the males were within the interval, 9.6-10.9 inches (200-229 millimeters), and 979 or 76.0 per cent of the females fell within the range, 10.1-11.4 inches (210-239 millimeters). In the distribution for the sexes combined 58.0 per cent of the fish were included in the interval, 10.1-10.9 inches (210-229 millimeters), and 88.3 per cent were from 9.6 inches (200 millimeters) to 11.4 inches (239 millimeters) long.

More detailed information on the length-frequency distribution and average size of kiyis, especially as related to the size of mesh of gill nets, may be found in Table 6. In order to present the frequencies in a table of reasonable size the data for the sexes have been combined, although where the samples were large the males averaged smaller and had lower modal lengths than did the females. These sex differences were much the same as those to be observed in the totals at the right of Table 5. The combination of data for the sexes should not affect the comparison of figures for nets of different mesh since males were generally scarce and no clear-cut or consistent relationship could be found between mesh size and the sex ratio (p. —).

It should be mentioned also that the frequencies were not based on actual measurements of all the fish listed but were estimated by the application of the percentage-frequency distributions as determined from samples from nets of the various mesh sizes to the corresponding total numbers of kiyis captured in lifts in which the fish were identified from nets of all (5 or 3) mesh sizes.[8] This procedure was made desirable by the variation in the percentage of fish measured from the total catch of nets of different mesh size (for example, a smaller percentage was measured from fish taken by the 2⅜-inch-mesh nets than from the catch of nets of any other mesh). In the following discussion the data for the five-net gangs of 1930-1931 will be treated first.

In spite of the rather large total ranges of length of kiyis in the gill

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[8]Numbers of fish actual'y measured are shown in the second row of the bottom section of the table. In some of the la-gest lifts it was necessary to restrict the identification of chubs to a sample. For these lifts the total number in the catch f-om a particular mesh size was estimated by multiplying the number of kiyis in the sample by the ratio of the number of chubs in the total lift to the number in the sample.

TABLE 6.—*Length frequencies of all kiyis captured and identified from Lake Michigan, 1930-1932*

[The frequencies were computed from the distributions of samples of measured fish. The total lengths in the second column are equivalent to the midpoints of the intervals of standard length. The gill-net meshes a.e extension measure in inches as manufactured]

| Standard length (millimeters) | Total length (inches) | Gill-net mesh in 1930-1931 | | | | | | | Gill-net mesh in 1932 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2% | 2½ | 2% | 2% | 3 | Total | Per-centage | 2½ | 2% | 2% | Total | Per-cent-age |
| 140-149 | 6.9 | .... | 3 | .... | .... | 2 | .... | ¹0.0 | .... | 2 | .... | 2 | 0.1 |
| 150-159 | 7.4 | .... | .... | .... | .... | .... | .... | .... | .... | .... | .... | 2 | 0.1 |
| 160-169 | 7.9 | 9 | .... | 2 | 2 | 4 | 17 | 0.1 | .... | 2 | .... | 2 | 0.1 |
| 170-179 | 8.4 | 19 | 3 | 5 | 6 | 12 | 45 | 0.3 | 3 | 3 | .... | 6 | 0.2 |
| 180-189 | 8.8 | 65 | 23 | 25 | 18 | 17 | 148 | 1.0 | 4 | .... | 2 | 9 | 0.3 |
| 190-199 | 9.3 | 537 | 95 | 49 | 44 | 57 | 782 | 5.2 | 30 | 25 | 16 | 71 | 2.7 |
| 200-209 | 9.8 | 2,307 | 400 | 199 | 69 | 65 | 3,040 | 20.3 | 85 | 36 | 28 | 149 | 5.6 |
| 210-219 | 10.3 | 3,326 | 1,014 | 360 | 107 | 29 | 4,836 | 32.3 | 282 | 92 | 30 | 404 | 15.2 |
| 220-229 | 10.7 | 2,168 | 1,070 | 458 | 157 | 21 | 3,874 | 25.9 | 571 | 244 | 70 | 885 | 33.4 |
| 230-239 | 11.2 | 667 | 486 | 301 | 145 | 9 | 1,608 | 10.8 | 361 | 250 | 82 | 693 | 26.2 |
| 240-249 | 11.6 | 148 | 141 | 122 | 64 | 9 | 484 | 3.3 | 130 | 127 | 66 | 323 | 12.2 |
| 250-259 | 12.1 | 19 | 40 | 20 | 23 | 2 | 104 | 0.7 | 26 | 31 | 30 | 87 | 3.3 |
| 260-269 | 12.6 | .... | 3 | 5 | .... | 2 | 12 | 0.1 | 2 | 3 | 4 | 9 | 0.3 |
| 270-279 | 13.1 | .... | 3 | .... | .... | 4 | 7 | ¹0.0 | 2 | .... | 2 | 4 | 0.2 |
| 280-289 | 13.5 | .... | .... | .... | 2 | .... | 2 | ¹0.0 | 2 | .... | .... | 2 | 0.1 |
| Total | | 9,265 | 3,281 | 1,546 | 637 | 235 | 14,964 | .... | 1,500 | 818 | 330 | 2,648 | .... |
| Number measured | | 2,556 | 1,361 | 773 | 321 | 112 | 5,123 | .... | 864 | 453 | 185 | 1,502 | .... |
| Average total length | | 10.3 | 10.5 | 10.5 | 10.6 | 9.9 | 10.4 | .... | 10.7 | 10.9 | 10.9 | 10.8 | .... |
| Ave age standard length | | 214 | 220 | 221 | 222 | 206 | 217 | .... | 224 | 228 | 230 | 226 | .... |

¹Less than 0.05.

nets of the five mesh sizes fished in 1930-1931, the ranges over which fish were taken in abundance were relatively small. Computations of percentage frequencies for the individual nets will show, for example, that the modal centimeter ($\frac{1}{2}$-inch[9]) interval contained from 35.9 per cent ($2\frac{3}{8}$-inch mesh) to 24.6 per cent ($2\frac{3}{4}$-inch mesh) of the total numbers of kiyis captured. Furthermore, the best represented 3-centimeter (1.4-inch) interval included from 84.2 per cent ($2\frac{3}{8}$-inch mesh) to 64.2 per cent ($2\frac{3}{4}$-inch mesh) of the total.

The variations among the average lengths of kiyis from nets of different mesh size were surprisingly small. The increase of mesh size from $2\frac{3}{8}$ to $2\frac{1}{2}$ inches was accompanied by a 6-millimeter (0.2-inch) rise in the average length. The mode also shifted 10 millimeters (from 210-219 millimeters to 220-229 millimeters). The differences among the $2\frac{1}{2}$-, $2\frac{5}{8}$-, and $2\frac{3}{4}$-inch meshes, however, were unimportant. The modal lengths were the same for all three nets (220-229 millimeters) and the maximum variation among the average lengths was only 2 millimeters (0.1 inch). The net with the largest mesh (3 inches) took the kiyis with the lowest modal (200-209 millimeters) and average (206 millimeters; 9.9 inches) lengths. This odd situation is the result of the capture of numbers of small individuals (termed "snipes" by the commercial fishermen) that were not gilled but were held by the mouth parts that had become entangled in the webbing.

Where the average and modal lengths varied but little, the numbers of kiyis captured by the chub gill nets decreased rapidly with increase in the size of the mesh ($\frac{1}{8}$-inch increases except the 3-inch mesh which was $\frac{1}{4}$ inch larger than the next smaller size). These decreases, expressed as percentages, were found to range from 64.6 per cent (from $2\frac{3}{8}$- to $2\frac{1}{2}$-inch meshes) to 52.9 per cent (from $2\frac{1}{2}$- to $2\frac{5}{8}$-inch meshes). Particularly noteworthy are the comparisons among the three intermediate mesh sizes. The $2\frac{1}{2}$-inch-mesh nets took kiyis that were only 1 millimeter shorter than those captured by the $2\frac{5}{8}$-inch-mesh nets (difference in total length is nil when expressed to the nearest 0.1 inch) but took 2.1 times as many individuals. The average lengths of kiyis from the $2\frac{5}{8}$- and $2\frac{3}{4}$-inch-mesh nets exhibited a similar difference (1 millimeter; 0.1 inch) but the former net captured 2.4 times as many fish as the latter. Finally, the $2\frac{1}{2}$-inch-mesh nets held 5.2 times as many kiyis as the $2\frac{3}{4}$-inch-mesh nets although the difference between the average lengths was only 2 millimeters (0.1 inch).

For the mesh sizes fished and for the stock of kiyis available in 1930 and 1931, therefore, the effect of gill-net selection was much more evident in the numbers of fish taken than in the sizes of individuals in the samples. In the combined samples of the nets of all five mesh sizes as in the collections from the individual meshes the bulk of the kiyis fell within a rather limited range of length. The modal-

[9]One centimeter of standard length corresponds to approximately 0.48 inch of total length—see page 107.

(half-inch) interval of 210-219 millimeters (equivalent midpoint, 10.3 inches) included 32.3 per cent of the total number of kiyis captured; 78.5 per cent of the total fell within the interval. 9.6-10.9 inches (200-229 millimeters). The grand average length of all kiyis captured in 1930-1931 was 10.4 inches (217 millimeters).

Comparisons of the 1932 data for northern Lake Michigan with the 1930-1931 data for southern Lake Michigan indicate a greater relative abundance of the larger kiyis in the northern area. It may be pointed out first that in 1932 the average lengths of the kiyis were consistently greater (4 to 8 millimeters; 0.2 to 0.4 inch) than those of fish captured by gill nets of corresponding mesh size in 1930-1931. Second, the length distribution of kiyis on the grounds was such as to permit successive increases of 4 and 2 millimeters (0.2 and 0.0 inch[10]) in average length with increase in mesh size as compared with corresponding rises of only 1 millimeter in 1930-1931. The increase in length of fish from the 2⅝-inch mesh over that of fish from the 2½-inch mesh was sufficiently great to involve a shifting of the mode from 220-229 millimeters to 230-239 millimeters. The mode remained at the latter interval, however, in the distribution of the kiyis from the 2¾-inch-mesh nets (possibly because of a scarcity of fish of sizes that could be taken most readily in these nets).

In northern Lake Michigan as in southern Lake Michigan the numbers of kiyis captured decreased sharply with increase in mesh size. The data for the northern region agree further with those of the southern in that the frequency distribution of the combined samples from nets of all mesh sizes fished was compact. More than one-third (33.4 per cent) of the total number of fish fell in the modal interval (220-229 millimeters; equivalent midpoint, 10.7 inches), and 74.8 per cent came within the length range of 10.1-11.4 inches (210-239 millimeters). The grand average length of all kiyis captured was 10.8 inches (226 millimeters). This average was 0.4 inch (9 millimeters) greater than that for kiyis from nets of five mesh sizes in 1930-1931 and 0.3 inch (5 milimeters) greater than the average for 1930-1931 samples from the same three mesh sizes fished in 1932.

The largest kiyi (longest and heaviest) measured was a spent male that was 13.8 inches (287 millimeters) long and weighed 11.7 ounces (332 grams). This fish was captured off Kewaunee, Wisconsin, on November 5, 1931. The largest female, a ripe fish which was taken off Racine, Wisconsin, on October 30, 1931, was nearly as heavy (11.6 ounces; 329 grams) but was shorter (13.2 inches; 277 millimeters). Both of these fish were well above the maximum size reported for the Lake Michigan kiyi by Koelz (1929) who stated, "Extreme examples selected from hundreds of specimens in the field measure only 245 millimeters [standard length; 11.7 inches total length]."

The total lengths given in this paper other than the average lengths

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[10]The total lengths corresponding to standard lengths of 228 and 230 millimeters are slightly more than 10.85 inches and slightly less than 10.95 inches respectively.

for age groups at capture and lengths of individual fish were computed by means of conversion factors determined from the measurements of the total and standard lengths of 6.017 kiyis. These factors for the conversion of standard lengths in millimeters to total lengths in inches were: 0.0479 for standard lengths up to 220 millimeters; 0.0476 for standard lengths of 220 millimeters or greater.

### COMPARISON OF THE GROWTH OF THE KIYI IN LAKES MICHIGAN AND ONTARIO

Average lengths and weights of age-groups II to VI of the Lake Ontario kiyi given by Pritchard (1931) permit a comparison of the growth of the species in two of the Great Lakes (Table 7). Since Pritchard made no separation of the data for the sexes, the lengths and weights of the males and females have been combined to obtain the averages given in the table for the age groups of the Lake Michigan kiyi. Only standard lengths have been presented as the total lengths of the Lake Ontario fish were measured to the fork of the tail while those of the Lake Michigan kiyis were measured to the extreme tip of the tail (with the upper and lower edges parallel). The younger age groups of the Lake Michigan kiyi (II and III) averaged larger and the older age groups (IV to VI) averaged smaller than fish of corresponding age from Lake Ontario. According to these figures, therefore, the Lake Michigan kiyis grew the more rapidly in the early years of life and the Lake Ontario kiyis had the better growth in the later years.

TABLE 7.—*Comparison of the average standard lengths and weights of the age groups of kiyis in Lake Michigan and Lake Ontario*

[The data for the Lake Ontario kiyis are from Pritchard (1931)]

| Age group | Lake Michigan | | Lake Ontario | |
|---|---|---|---|---|
| | Length (millimeters) | Weight (grams) | Length (millimeters) | Weight (grams) |
| II | 210 | 137 | 178 | 82 |
| III | 211 | 139 | 203 | 125 |
| IV | 218 | 153 | 222 | 167 |
| V | 224 | 164 | 241 | 207 |
| VI | 229 | 175 | 274 | 302 |

Several circumstances throw doubt on the data of Table 7 as a reliable measure of differences in the growth rates of the kiyis in the two lakes. First may be mentioned differences in the experimental gear employed. Seventy per cent of the 524 kiyis captured in experimental gill nets in Lake Ontario were taken in meshes that were smaller (four mesh sizes from 1¼ to 2¼ inches) than any fished in Lake Michigan (five mesh sizes from 2⅜ to 3 inches). The three mesh sizes (2½, 2¾, and 3 inches) that were fished in Lake Ontario and that came within the range fished in Lake Michigan took 25.6 per cent of the kiyis, while nets of five larger mesh sizes (3½ to 5 inches) captured the remaining 4.4 per cent. It seems likely that Pritchard's samples had the better representation of the smaller fish and hence

of the younger age groups. That the representation of the larger fish (in relation to the population present) was much better in the Ontario than in the Michigan samples seems doubtful in view of the small numbers of individuals from the Ontario nets with mesh sizes greater than those of nets fished in Lake Michigan (most probably a consid- erable proportion of the kiyis from the largest meshes fished by Pritch- ard were "accidental" captures of fish held by their mouth parts) and of the evidence of the preceding section that the Michigan nets could have taken longer fish had they been available.

Attention should be called also to the extremely intensive fishery in Lake Michigan that tended to eliminate the individuals with the more rapid growth and hence to cause the samples of the successively older age groups to include an increasing percentage of individuals with growth rates below the normal (p. 100).

Differences in the growth rates of the sexes together with differences in the sex ratio in the two lakes may account for some of the dis- crepancies.

Finally, part of the disagreements may be the result of the inade- quate numerical representation of certain age groups. (Pritchard did not give the numbers of specimens upon which the averages for the age groups were based—see Table 2 for the numbers in the age groups of the Lake Michigan kiyi.)

From the preceding considerations it seems likely that the differ- ences between the growth of the kiyi in Lake Michigan and in Lake Ontario may not be as great as would appear from the data of Table 7. It is particularly significant that the best agreement is to be found in the data for age-group IV which was probably one of the most ade- quately represented groups in the Lake Michigan collections.

CALCULATED GROWTH IN LENGTH AND WEIGHT

*Growth of the age groups and general growth in length.*—The com- bination of the data for all collections to obtain the growth histories of the age groups and the general growth for all age groups combined (Tables 8 and 9) was made only after careful comparisons of the data

TABLE 8.—*Calculated lengths of each age group of male kiyis and grand average calculated lengths*

[The data for all collections have been combined]

| Age group | Number of fish | Calculated standard length (millimeters) at end of year of life | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| II ..................... | 7 | 112 | 171 | ...... | ....... | ....... | ....... | ....... |
| III ..................... | 37 | 99 | 144 | 179 | ....... | ....... | ....... | ....... |
| IV ..................... | 71 | 101 | 143 | 174 | 197 | ....... | ....... | ....... |
| V ..................... | 44 | 97 | 136 | 166 | 186 | 202 | ....... | ....... |
| VI ................. .. | 11 | 96 | 137 | 163 | 180 | 197 | 211 | ....... |
| VII ................. | 2 · | 94 | 136 | 168 | 189 | 202 | 210 | 221 |
| Average ........................... | | 100 | 142 | 172 | 192 | 201 | 211 | 221 |
| Increment ......................... | | 100 | 42 | 30 | 20 | 9 | 10 | 10 |
| Total length (inches)...... | | 4.8 | 6.8 | 8.2 | 9.2 | 9.6 | 10.1 | 10.5 |
| Increment ......................... | | 4.8 | 2.0 | 1.4 | 1.0 | 0.4 | 0.5 | 0.4 |
| Number of fish ................ | | 172 | 172 | 165 | 128 | 57 | 13 | 2 |

TABLE 9.—Calculated lengths of each age group of female kiyis and grand average calculated lengths

[The data for all collections have been combined]

| Age group | Number of fish | Calculated standard length (millimeters) at end of year of life | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| II | 26 | 113 | 175 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... |
| III | 154 | 103 | 147 | 189 | ..... | ..... | ..... | ..... | ..... | ..... | ..... |
| IV | 569 | 102 | 144 | 180 | 202 | ..... | ..... | ..... | ..... | ..... | ..... |
| V | 486 | 104 | 143 | 178 | 198 | 215 | ..... | ..... | ..... | ..... | ..... |
| VI | 192 | 101 | 137 | 171 | 193 | 208 | 222 | ..... | ..... | ..... | ..... |
| VII | 43 | 105 | 136 | 164 | 186 | 203 | 216 | 227 | ..... | ..... | ..... |
| VIII | 6 | 107 | 133 | 158 | 182 | 196 | 208 | 220 | 231 | ..... | ..... |
| X | 1 | 81 | 119 | 140 | 158 | 169 | 179 | 192 | 203 | 214 | 222 |
| Average | | 103 | 143 | 179 | 199 | 212 | 220 | 225 | 227 | 214 | 222 |
| Increment | | 103 | 40 | 36 | 20 | 13 | 8 | 5 | 2 | −13 | 8 |
| Total length (inches) | | 4.9 | 6.8 | 8.6 | 9.5 | 10.2 | 10.5 | 10.7 | 10.8 | 10.2 | 10.6 |
| Increment | | 4.9 | 1.9 | 1.8 | 0.9 | 0.7 | 0.3 | 0.2 | 0.1 | −0.6 | 0.4 |
| Number of fish | | 1,477 | 1,477 | 1,451 | 1,297 | 728 | 242 | 50 | 7 | 1 | 1 |

for the individual samples. These comparisons did reveal certain differences in the calculated growth of kiyis in the different collections. The variations resembled those indicated earlier in Tables 3 and 4. When the fish of the 2⅜- and 3-inch-mesh nets were eliminated from the 1931 samples to make them more nearly comparable with the 1932 collections the general agreement among the average calculated lengths of the kiyis of the several localities was improved. The statement made earlier (p. 100) that some of the variations in the size of the fish of corresponding age groups at capture might represent true local differences in growth rate may well apply to the calculated lengths. On the other hand, the same distorting factors (discussed on pp. 97-100) that could have affected the length of the kiyis at capture would also influence the calculated lengths.[11] These factors made so uncertain the real significance of observed differences in growth rate that the combination of the data for all localities appeared to provide the best available measure of the growth in length of the Lake Michigan kiyi.

One possible local difference in the rate of growth in length may be mentioned, however. The first-year calculated lengths of the kiyis from northern Lake Michigan (Manistique and the Fox Islands) were rather consistently higher than those of fish of the same age from other localities. The difference was not large (average of roughly 4 or 5 millimeters) but by reason of its rather consistent occurrence well may be significant.

The discrepancies among the calculated lengths of the age groups (all collections combined) were at times large. These disagreements differed from those typical of "Lee's phenomenon" in that the later rather than the earlier years of life were affected most severely. If the data for age-group II are excepted it can be said that discrepancies between successive age groups were, in general, small for first-year lengths,[12] considerably larger for second-year lengths, and most severe for calculated lengths beyond the second year.

It is not believed that errors due to faults in the method of calculating growth were an important source of the discrepancies in Tables 8 and 9. Although Van Oosten (1929) did find that lengths computed by direct proportion from diameter measurements were not perfectly accurate in the related species, *Leucichthys artedi*, the disagreements that occurred were so small that he held the method to be satisfactory for practical purposes. Furthermore, the discrepancies found by Van Oosten affected chiefly the early rather than the late years of life.

Errors of age determination traceable to the presence of accessory

[11]An exception must be made, of course, for the effects of the time of capture in the growing season.
[12]The validity of this statement is not affected by the distortion brought about by the high first-year lengths of kiyis from northern Lake Michigan. When the samples from the Manistique and Fox Islands areas were excluded the first-year lengths of the female kiyis of the remaining collections were found to be 101 for age-groups III, IV, and V, 96 for age-group VI, and 99 for age-group VII. Similar computations for the males showed an increase in the total range of variation of $l_1$ (age-groups III-VI) from 96-101 to 95-101.

checks, so prominent that they were taken as annuli, could have contributed to the discrepancies. Although the reading of the kiyi scales was sufficiently difficult that some incorrect readings almost certainly were made, the number of errors must have been reduced greatly by the discarding of the most difficult scales (more than 5 per cent in northern Lake Michigan samples which contained relatively more old fish). An even stronger argument against errors of age determination as an important source of the discrepancies is to be found in the circumstance that disagreements were present among the second-year lengths and severe among the third-year lengths although the detection of the first three annuli presented a simple problem on almost all scales.

Although the factors just discussed conceivably may have been responsible for some small part of the discrepancies in Tables 8 and 9, it is believed these disagreements can be explained more satisfactorily as the result of gill-net selection and differences in the mortality rate of kiyis with different rates of growth.[13]

The extremely high calculated lengths of age-group II can be attributed primarily to the selection by the gill nets of the larger individuals with the more rapid growth. The relatively poor representation of age-group III in comparison with age-group IV suggests that here too selection took place and the smaller fish with the slower growth rate were not adequately represented in the former group. The effect of gill-net selection on the average calculated lengths of the older age groups is more difficult to judge. The small variations among the length-frequency distributions of the age groups (Table 5) give cause to believe, however, that the representation of the smaller individuals may have been inadequate also in some age groups beyond the III group. The severity of the selection obviously would decrease with increase in age. There is no reason to believe that any of the discrepancies among the very oldest age groups were the result of the selection by the nets of the slowly growing individuals of those ages. If members of these age groups that were larger and faster growing than those taken had been present in the lake they could have been captured by the 2¾- and 3-inch-mesh nets. These nets, however, took relatively few kiyis (Table 6).

When, as with chubs, there is an intensive commercial fishery the capture by the gill nets of the larger members of certain age groups not only serves as a source of bias in the samples but also brings about a gradual modification of the stock with respect to the growth rate of the individuals present. If the gill nets take the larger members of an age group and if, as suggested in the preceding paragraph, this selection affects the members of a single year class year after year (that is, occurs in several age groups) it is inevitable that even perfectly random samples of the fish remaining in the lake will show a diminishing growth rate with each older age group.

[13] Numerous explanations of discrepancies in calculated lengths in addition to those mentioned here can be found in the literature. The present discussion, however, will deal only with factors considered most pertinent to the problem presented by the data for the kiyi.

A greater mortality of the fish with the more rapid growth possibly may occur independently of the destruction by the fishery of the larger members of certain age groups. The calculated lengths of the Silver Lake (Wisconsin) cisco, *Leucichthys artedi*, exhibited discrepancies that resembled closely those shown by the kiyi (Hile, 1936). In Silver Lake, however, the cisco had not been subjected to any fishing mortality at all. After a consideration of the possible sources of the discrepancies Hile concluded that the natural mortality rate of Silver Lake ciscoes that grew rapidly was greater than that of the individuals whose growth was slow. As a result of this correlation of growth rate and length of life each successively older age group was composed of fish with slower and slower growth.

An illustration of the manner in which a higher mortality rate for fish with the more rapid growth can produce discrepancies in calculated lengths similar to those observed in the kivi is provided by Table 10 which brings out the effect of eliminating the 46 fish above the average size on the determination of the growth history of the V-group females in the Manistique collection of June 14, 1932. When these larger fish were excluded from the sample the agreement between the corresponding calculated lengths of age-groups V and VI was well-nigh perfect.

TABLE 10.—*Effect of the elimination of fish with the more rapid growth on the determination of the calculated lengths of the V-group female kiyis of the Manistique collection of June 14, 1932*

[For comparison, the growth history of the VI-group females is given at the bottom of the table]

| Age group | Sample | Number of fish | Length at capture | Calculated standard length (millimeters) at end of year of life | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | 1 | 2 | 3 | 4 | 5 | 6 |
| V | All in age group............ | 98 | 225 | 107 | 145 | 181 | 201 | 220 | ...... |
| V | Fish longer than 225 millimeters omitted.... | 52 | 216 | 103 | 138 | 173 | 193 | 211 | ...... |
| VI | All in age group............ | 54 | 229 | 102 | 138 | 174 | 194 | 210 | 225 |

Regardless of possible uncertainty as to the underlying causes, it is obvious that individual rate of growth and individual length of life are correlated (negatively) in the Lake Michigan kivi. The resulting fundamental differences in the growth histories of the various age groups diminish the value of a general growth curve derived from the combination of the data for fish of all ages. Certain of the observations made by Hile (1936) on this problem with respect to the Silver Lake cisco apply equally well to the Lake Michigan kivi:

> The Silver Lake growth data raise a question as to the value and significance of any "general" growth curve in this population. The presentation of a general growth curve involves the tacit assumption that this curve can be taken to represent the course of growth of an individual that is typical of the population as a whole. However, the Silver Lake growth curve was derived from the combination of several age groups whose growth histories were fundamentally different. It appears characteristic of the Silver Lake cisco that individual growth history and individual life span are definitely

correlated. Consequently the combining of all age groups to obtain a general growth curve involves the lumping together of a mass of heterogeneous growth material. The typical individual that such a curve is purported to represent is probably non-existent.

In spite of the defects inherent in the data, the determination of the "general" growth in length of the kiyi seems to be desirable. With the kiyi as with the Silver Lake cisco this general curve probably does not represent the growth of a typical individual. It does, however, provide a picture of the composite growth histories of the heterogeneous materials that came from a heterogeneous population.

No age groups were excluded in the computation of the averages at the bottom of Tables 8 and 9 although the calculated lengths of the II groups and probably of some older age groups as well were too high as the result of gill-net selection. It was believed that the retention of·the data for the younger age groups would compensate in some measure the increasingly inadequate representation of the more rapidly growing individuals in the older age groups. The growth in length has been presented graphically for the first 8 years of life (only 7 years for the males) in Figure 1.

The growth of the kiyi is extremely slow. At the end of 4 full years the calculated lengths of both males and females were substantially less than 10 inches. In fact, this length was not attained by the males until the sixth year of life. At the end of 7 years the calculated length of the males was 10.5 inches (221 millimeters); at the end of 8 years the calculated length of the females was 10 8 inches (227 millimeters). Because of the slow growth of the single X-group fish the ninth- and tenth-year calculated lengths of the females were lower than those for the seventh and eighth years. Beyond the second year of life the calculated lengths of the females were 0.2 to 0.6 inch (4 to 11 millimeters) greater than those of the males.

Kivis of both sexes made by far their best growth in length during the first year of life (nearly 5 inches; about 100 millimeters). The growth rate declined sharply in the second year when the increment of about 2 inches (40-42 millimeters) was less than half that of the first year. The gradual decrease in the later years led to extremely low values of the increments. Fish of neither sex had increments of more than an inch (20 millimeters) in any year beyond the third. In the males the fifth-, sixth-, and seventh-year increments·were nearly the same and did not exceed a half inch (9-10 millimeters). The length increment of the females dropped to the even lower value of 0.1 inch (2 millimeters) in the eighth year.

*General growth in weight.*—The calculated weights for kivis of the central basins of Lake Michigin and of the Fox Islands district (Table 11 and Fig. 2). which were determined by means of the length-weight equations given on p. 124, correspond exactly with the grand average calculated lengths of Tables 8 and 9. It seemed desirable (in order to facilitate comparisons) to base computations of growth in weight of the fish from the two areas on the grand average calculated
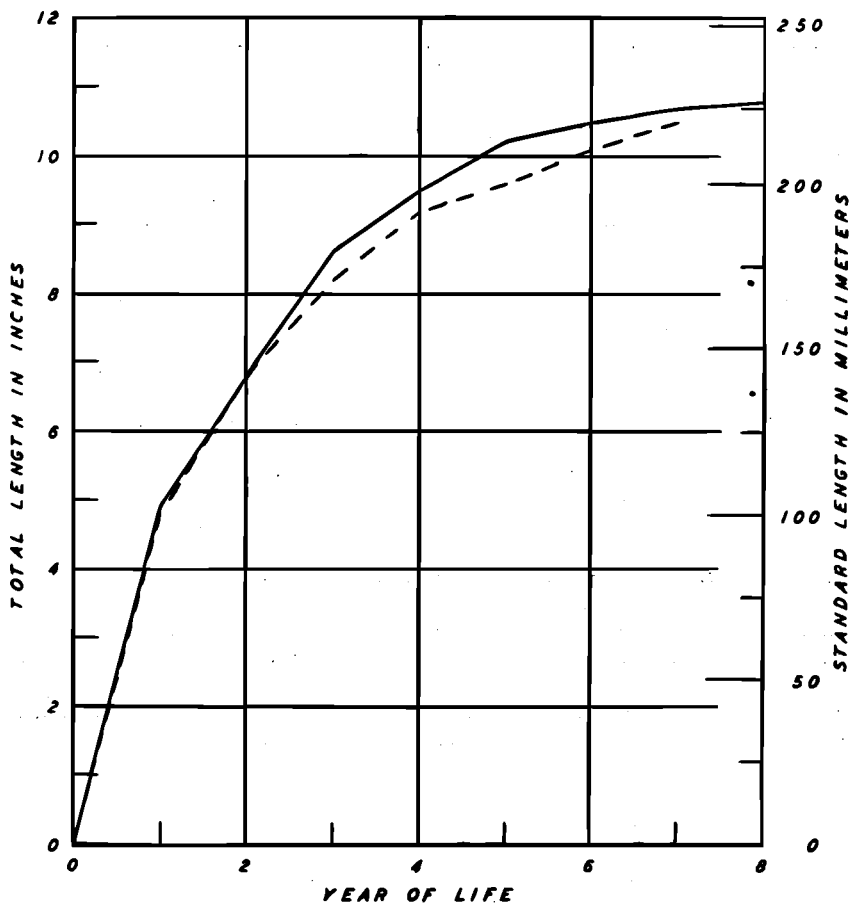
FIGURE 1.—Calculated growth in length of the Lake Michigan kiyi. Solid line, females; broken line, males.

lengths of the combined samples from these areas. This procedure is valid since the growth in length of kiyis apparently was approximately the same in both regions.

In both areas of Lake Michigan the growth in weight was slow. The maximum annual increment of calculated weight, which occurred without exception in the third year of life, was as low as 1.03 ounces or 29 grams (males, Fox Islands) and did not exceed 1.38 ounces or 39 grams (females, central basins of lake). The fourth-year increases of the females were just over 1 ounce but all other increments were less than an ounce. This slow growth is reflected in the amount of time required to attain certain weights. The females did not attain a

TABLE 11.—*Calculated growth in weight of Lake Michigan kiyis*

[The weights, which correspond exactly to the grand average calculated lengths of Tables 8 and 9, were computed by means of the equations given on p. 124]

| Year of life | Males | | | | Females | | | |
|---|---|---|---|---|---|---|---|---|
| | Weight (g.ams) | Incre-ment | Weight (ounces) | Incre-ment | Weight (grams) | Incre-ment | Weight (ounces) | Incre-ment |
| | Central basins of Lake Michigan | | | | | | | |
| 1 | 13 | 13 | 0.46 | 0.46 | 14 | 14 | 0.49 | 0.49 |
| 2 | 39 | 26 | 1.38 | 0.92 | 40 | 26 | 1.41 | 0.92 |
| 3 | 70 | 31 | 2.47 | 1.09 | 79 | 39 | 2.79 | 1.38 |
| 4 | 98 | 28 | 3.46 | 0.99 | 109 | 30 | 3.84 | 1.05 |
| 5 | 113 | 15 | 3.99 | 0.53 | 133 | 24 | 4.69 | 0.85 |
| 6 | 131 | 18 | 4.62 | 0.63 | 149 | 16 | 5.26 | 0.57 |
| 7 | 151 | 20 | 5.33 | 0.71 | 160 | 11 | 5.64 | 0.38 |
| 8 | ...... | ...... | ...... | ...... | 164 | 4 | 5.78 | 0.14 |
| 9 | ...... | ...... | ...... | ...... | 137 | −27 | 4.83 | −0.95 |
| 10 | ...... | ...... | ...... | ...... | 153 | 16 | 5.40 | 0.57 |
| | Fox Islands Area | | | | | | | |
| 1 | 12 | 12 | 0.42 | 0.42 | 13 | 13 | 0.46 | 0.46 |
| 2 | 35 | 23 | 1.23 | 0.81 | 36 | 23 | 1.27 | 0.81 |
| 3 | 64 | 29 | 2.26 | 1.03 | 73 | 37 | 2.57 | 1.30 |
| 4 | 91 | 27 | 3.21 | 0.95 | 102 | 29 | 3.60 | 1.03 |
| 5 | 105 | 14 | 3.70 | 0.49 | 124 | 22 | 4.37 | 0.77 |
| 6 | 122 | 17 | 4.30 | 0.60 | 140 | 16 | 4.94 | 0.57 |
| 7 | 142 | 20 | 5.01 | 0.71 | 150 | 10 | 5.29 | 0.35 |
| 8 | ...... | ...... | ...... | ...... | 154 | 4 | 5.43 | 0.14 |
| 9 | ...... | ...... | ...... | ...... | 128 | −26 | 4.51 | −0.92 |
| 10 | ...... | ...... | ...... | ...... | 144 | 16 | 5.08 | 0.57 |

calculated weight of a quarter pound before the fifth year of life or the males before the sixth. The females from the central basins of Lake Michigan required more than five growing seasons to reach a weight of 5 ounces while the females from the Fox Islands region and the males from both areas needed more than 6 years to attain that weight.

The annual increments of weight of kiyis of both sexes from both regions of Lake Michigan increased from the first to the third year. Thereafter the increments of the males varied irregularly (decrease in the fifth year; increases in the sixth and seventh years). The weight increments of the female kiyis declined from the fourth through the ninth years of life (were, in fact, negative in the ninth year) but amounted to more than a half ounce in the tenth. Little dependence can be placed, however, on the calculated weights of the females for the ninth and tenth years since they were based on the calculated lengths of a single X-group fish.

The differences between the corresponding calculated weights of kiyis from the central basins of Lake Michigan and from the Fox Islands area can be attributed to the more slender body form of the fish from the northeastern island region. Male kiyis from the former waters were 0.04 ounce (first year) to 0.32 ounce (sixth and seventh years) heavier than males of corresponding age from the latter region. The advantage of the females from the central basins of Lake Michigan ranged from 0.03 ounce (first year) to 0.35 ounce (seventh and eighth years).
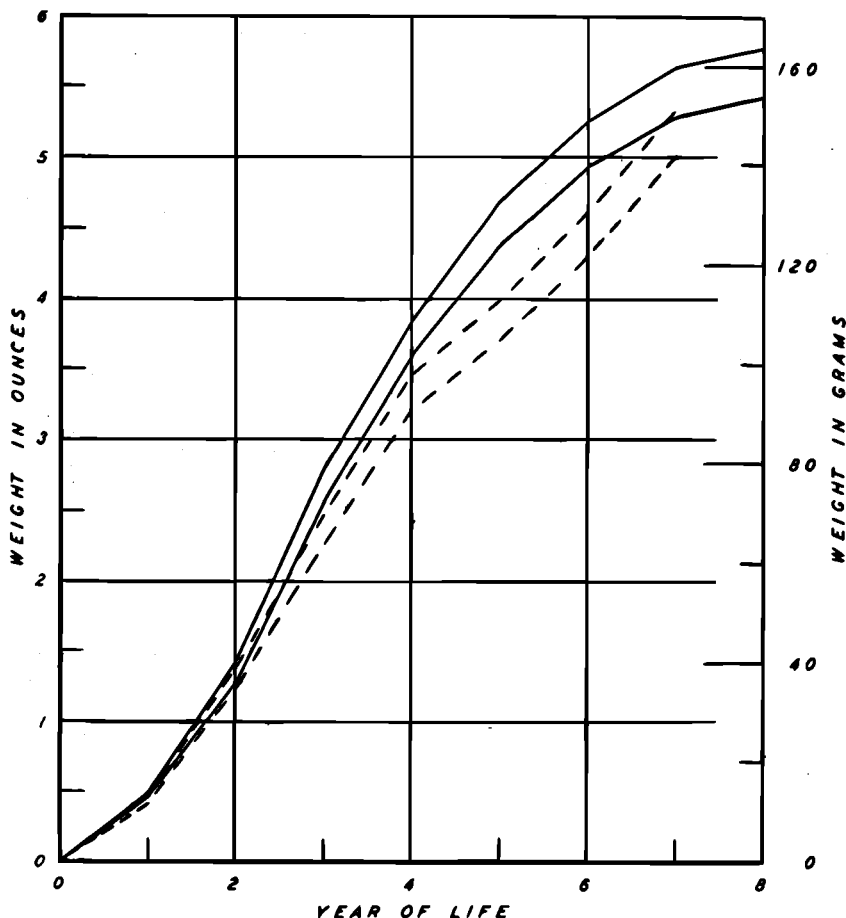
FIGURE 2.—Calculated growth in weight of female (solid line) and male (broken line) kiyis in the central basins of Lake Michigan (upper curves) and in the Fox Islands region (lower curves).

## GROWTH COMPENSATION

Growth compensation—the tendency for the smaller young fish to grow more rapidly in the later years of life than do the larger young fish—appears to be characteristic of most coregonids. Growth compensation was observed in the lake herring or cisco (*Leucichthys artedi*) by Van Oosten (1929) and Hile (1936), in the Lake Superior longjaw (*L. zenithicus*) by Van Oosten (1937), in Reighard's chub (*L. reighardi*) of Lake Michigan by Jobes (1943), and in the Lake Huron whitefish (*Coregonus clupeaformis*) by Van Oosten (1939). The phenomenon was not found, however, by McHugh (1941) in any

TABLE 12.—*Relationship between first-year standard length (millimeters) and later growth in length of IV-group female kiyis of the Port Washington, Wisconsin, collection*

| Number of fish | Interval of calculated length in millimeters at end of first year | Calculated length at end of year of life | | | | | Calculated increment of length in year of life | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | '5 | 1 | 2 | 3 | 4 | '5 |
| 49 ............ | < 90 | 83 | 129 | 166 | 190 | 210 | 83 | 46 | 37 | 24 | 20 |
| 155 ............ | 90-109 | 100 | 141 | 177 | 199 | 215 | 100 | 41 | 36 | 22 | 16 |
| 63 ............ | >109 | 117 | 153 | 186 | 205 | 220 | 117 | 36 | 33 | 19 | 15 |
| Maximum difference .................. | | 34 | 24 | 20 | 15 | 10 | | | | | |

¹Incomplete season; fish captured on August 13 and 21, 1931.

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of the populations of the Rocky Mountain whitefish (*Prosopium williamsoni*) studied by him.

The calculated growth histories of three yearling size groups of IV-group females of the Port Washington, Wisconsin, collection (Table 12) indicate that the kiyi also exhibits growth compensation. Although the largest yearlings had the greatest length and the smallest yearlings the least length at the end of each subsequent year of life and at capture in the fifth summer, the advantage of the large over the small fish decreased each year (progressive decline of the "maximum difference" from 34 millimeters to 10 millimeters). The consistency with which growth compensation took place is brought out by the fact that without exception the size of the calculated annual increments of the three yearling size groups (at right of Table 12) followed the reverse order of the average first-year lengths.

AMOUNT OF SEASON'S GROWTH COMPLETED AT TIME OF CAPTURE

The best information on the increase in length during the growing season was supplied by the three 1932 collections from the Manistique area (Table 13). The calculated increments of length of female kiyis[14] from the time of the formation of the last annulus to the time of capture of the June 14 collection amounted to 39 per cent of the increments of the September 7 sample (the final collection of the year).

TABLE 13.—*Comparison of the amount of growth (increase of standard length in millimeters) made by female kiyis of five age groups in three collections from the Manistique region from the time of formation of the last annulus up to the time of capture*

[In parentheses, each increment is expressed as a percentage of the increment of the corresponding age group in the September collection]

| Date of capture | Age group | | | | | Average percentage |
|---|---|---|---|---|---|---|
| | III | IV | V | VI | VII | |
| June 14, 1932...... | 7 (39) | 6 (40) | 5 (45) | 4 (44) | 2 (25) | ...... 39 |
| July 9, 1932........ | 15 (83) | 12 (80) | 9 (82) | 6 (67) | 7 (88) | ...... 80 |
| Sept. 7, 1932........ | 18 (100) | 15 (100) | 11 (100) | 9 (100) | 8 (100) | ...... 100 |

On July 9 the kiyis had completed 80 per cent of the growth they would have been expected to make had they survived 2 months longer. Comparisons of the "partial growth" of kiyis captured in June and July indicate that 41 per cent of the total growth to September 7 was made in less than a month. The relatively small increase from July 9 to September 7 (20 per cent of the total growth to the latter date) suggests that growth was extremely slow in the latter part of the season or possibly was terminated earlier than September 7. Indeed, if

[14]Because of the scarcity of males in the collections, this section is based entirely on data for the females. There is no evidence that the course of the season's growth differs in the two sexes.

growth was as rapid or nearly as rapid after July 9 as between June 14 and that date the growing season must have come to an end in the latter part of July. If the growth rate declined gradually after July 9 the end of the season was delayed accordingly.

The lack of collections from the Manistique region later than September 7 makes it impossible to prove the tentative assumption of the preceding paragraph that the 1932 growth actually had been completed by that date (or earlier). Some information on the question can be obtained, nevertheless, from the comparison of the "partial growth" in 1932 up to September 7 with the full-season growth made in the corresponding year of life by members of the next higher age group[15] (Table 14). On first consideration these comparisons would seem to disprove rather than support the belief that the 1932 growth of kiyis from the Manistique area was complete in early September, for the partial growth was without exception less than the full-season growth. It should be remembered, however, that the partial growth was made in 1932 whereas the full-season increments were for 1931. If growth was better in 1931 than in 1932 the discrepancies may be

TABLE 14.—*Comparison of the growth (standard length in millimeters) of certain age groups of female kiyis from the time of formation of the last annulus up to the time of capture with the full-season growth made in the same year of life by fish of the next higher age group*

[Numbers of specimens in parentheses]

| Locality | Date of capture | Definition and year of increment | Age group from which partial growth was computed | | | | |
|---|---|---|---|---|---|---|---|
| | | | III | IV | V | VI | VII |
| Manistique .... | Sept. 7, 1932 | Growth in 1932 | 18 (2) | 15 (20) | 11 (89) | 9 (57) | 8 (.13) |
| | ............ | Full-season growth,[1] 1931 | 22 (62) | 17 (234) | 14 (143) | 11 (36) | 12 (4) |
| Fox Islands.... | Aug. 13, 1932 | Growth in 1932 | 10 (1) | 12 (15) | 9 (26) | 7 (10) | ...... |
| | ............ | Full-season growth, 1931 | 21 (15) | 16 (26) | 14 (10) | 11 (4) | ...... |
| Kewaunee .... | Oct. 15, 1931 | Growth in 1931 | 25 (49) | 18 (130) | 13 (63) | 12 (14) | ...... |
| | ............ | Full-season growth, 1930 | 21 (130) | 15 (63) | 13 (14) | 7 (1) | ...... |
| Port Washington ...... | Aug. 13 and 21, 1931 | Growth in 1931 | 19 (27) | 17 (267) | 12 (138) | 11 (20) | 8 (2) |
| | ............ | Full-season growth, 1930 | 22 (267) | 16 (138) | 13 (20) | 10 (2) | 13 (1) |
| Racine .......... | Oct. 9, 1931 | Growth in 1931 | 26 (63) | 19 (95) | 14 (25) | 12 (5) | ...... |
| | ............ | Full-season growth, 1930 | 23 (95) | 18 (25) | 13 (5) | 9 (1) | ...... |

[1]Determined from the combined collections of June 13, July 9, and Sept. 7, 1932.

[15]Comparisons between groups whose ages differ by more than one year are inadvisable because of the systematic discrepancies between the growth histories of kiyis of different age. Comparisons between consecutive age groups minimize but probably do not eliminate the distorting effects of these discrepancies.

the result of annual fluctuations in growth rate, and therefore not valid evidence for continued growth after September 7.

Although it can not be proved that the growth of the kiyi was better in 1931 than in 1932, comparisons of growth in 1931 and 1930 yield evidence that the 1931 growth may have been somewhat better than average (Table 14). The 1931 growth of kiyis of the Kewaunee and Racine collections captured during the spawning season (at which time the season's growth almost certainly had been completed) exceeded (with the single exception of the Kewaunee V group) the 1930 growth for the corresponding year of life (as computed from fish of the next higher age group). Since these advantages of 1931 over 1930 growth were of approximately the same magnitude as the discrepancies in the Manistique data between the 1931 full-season growth and the 1932 "partial growth" up to September 7, the possibility exists that the discrepancies in the Manistique material also can be attributed to annual differences in growth rate. Consequently, the advantage of the 1931 full-season increments of the Manistique kiyis over the 1932 partial growth for corresponding years of life does not necessarily invalidate the belief (based on the small increase from July 9 to September 7) that growth in 1932 had ended by early September and possibly may have been terminated at an earlier date.

Some additional information on the probable time at which the season's growth of kiyi is completed is provided by the data for the Fox Islands and Port Washington collections, both of which were made up of fish taken near the middle of August. Among the best represented age groups (IV to VI) of the Fox Islands sample the growth increments up to August 13 were 4 or 5 millimeters less than the full-season increments computed from the next higher age groups. To some extent the discrepancies may be the result of differences in growth rate in 1931 and 1932 (see preceding paragraphs). However, the fact that the differences were larger than those shown by the Manistique collection of September 7 gives evidence that growth in the Fox Islands area was not complete on August 13.

Comparisons of the increments for the Manistique and Fox Islands kiyis also suggest the existence of local differences in the course of the season's growth. Although the corresponding full-season increments for the Manistique and Fox Islands fish were nearly the same (Table 14), the Manistique kiyis of age-groups IV and V had grown as much by July 9 (Table 13) as the Fox Islands fish of the same age had grown by August 13 and the "partial growth" of the VI group at Manistique was only 1 millimeter lower than the "partial growth" of the VI group from the Fox Islands.

The 1931 growth of the Port Washington kiyis up to the time of capture in mid-August (August 13 and 21) differed but little from the full-season growth for the same year of life in 1930 ("partial growth" was the larger in age-groups IV and VI and the smaller in age-groups III, V, and VII). This agreement suggests that the 1931 growth had

been nearly if not fully completed by mid-August. It should be remembered, however, that the 1931 growth of kiyis taken later in the season off Kewaunee and Racine exceeded the 1930 growth for the corresponding year of life. If conditions off Port Washington were the same as those off the other two ports, a small amount of growth after mid-August might be expected.

The general conclusion seems warranted that all or most of the kiyi's growth is completed by the end of August. The time at which the growing season ends possibly may be subject to local and annual fluctuations. There is reason to believe, for example, that kiyis from the Fox Islands and Port Washington areas may have continued growth after mid-August while the Manistique data yielded evidence that growth may have ended as early as late July.

That the growth of coregonids can be completed at an early date was demonstrated by Hile (1936) who determined that the Trout Lake (Wisconsin) ciscoes captured at the end of July had completed substantially all of the current season's growth. One of the explanations advanced for the short growing season of the Trout Lake cisco (the seasons were longer for the cisco populations in three other lakes of the same region) was to the effect that the early termination of growth might be associated with an earlier development of the gonads (preliminary to spawning) in the slowly growing Trout Lake stock.

In the event that the cessation of growth and the onset of the pre-spawning development of the gonads are associated, an early end to the growing season of the kiyi would not be surprising since, according to Hile and Deason (1947), that species spawns rather early in Lake Michigan (peak of spawning activities in late October and early November) for an autmn-spawning coregonid. These authors also presented evidence that the development of the gonads preliminary to spawning may set in at an early date (July or August).

Definite information is lacking on the date at which the growth of the kiyi begins. The fish taken in the Manistique region on June 14 had completed 39 per cent of the growth they would have been expected to make had they survived till September 7. If the growth rate prior to June 14 could be assumed to be approximately the same as that between June 14 and July 9 the beginning of the season could be set a little later than the middle of May. If the early growth rate averaged slower than that between June 14 and July 9, the beginning of the growing season was earlier than the middle of May.

In spite of some uncertainties as to the dates at which the season's growth of the kiyi begins and ends, and in spite of the strong probability of some local and annual variation in these dates, the general conclusion that the growing season is in the neighborhood of 3-3½ months long probably comes near the truth.

If, as estimated above, the seasonal growth of the kiyi begins in May, the time of annulus formation is approximately normal for the latitude (Beckman, 1943). An intriguing question arises, however, con-

cerning the factor or factors that determine the time growth sets in, for the kiyi seems not to experience the sharp rise of water temperature that ordinarily marks the beginning of the growing season. Hile and Deason (1947) have pointed out that in May-November, inclusive, the bulk of the kiyi stock in southern and central Lake Michigan (and almost certainly in northern Lake Michigan also) lives at depths in which the water temperature varies only a fraction of a degree from 4° C. Although we know nothing of the bathymetric distribution of the kiyi between November and May, and information on the annual cycle of temperature changes is incomplete, especially in the great central basins in which most of the kiyis live, the data given by Church (1942) on winter temperatures along the Milwaukee-Muskegon route (this route lies across the shallows separating the two great basins) suggest that the spring rise in temperature of waters inhabited by the kiyi may not be much more than 2° C. (increase from 2° C. in winter to about 4° C. in summer). Church's data suggest also that the kiyi may encounter the highest temperatures of the year in the late fall and early winter. The readings for early and middle December, at which time the lake is vertically almost isothermal, showed temperatures of 5.75° C.-6.00° C. down to depths of about 60 fathoms and greater. In view of this unusual cycle, and the extremely small range of the temperature changes to which the kiyi is exposed, it would appear that if temperature is the factor controlling the seasonal course of growth, the kiyi must be sensitive to extremely small gradients in the spring and fail to react to equally large increases and absolutely higher temperatures in the early winter. More probably the time at which growth begins is determined by some other factor such as food or light.

## LENGTH-WEIGHT RELATIONSHIP

*Seasonal, annual, and local differences; general relationship.*—Tabulations of the length-weight data of the Lake Michigan kiyi were made originally according to sex, port, and month and calendar year of capture. During the period, May through September, the females were consistently slightly heavier than males of corresponding length. These sex differences usually were small, however (differences between the value of $K$[16] for males and females ordinarily ran less than 0.05) particularly in comparison with the larger monthly and annual fluctuations. (In the spawning period the extent of sex differences varied according to the state of the organs of the fish in the samples but generally were much larger than in summer; the length-weight relationship of spawning-run fish captured in October and November will be treated in some detail in the next part of this section but for immediate purposes the averages for all fish combined are adequate.) Consequently, the data for the sexes were combined for the study of

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[16]$K = \dfrac{W \times 10^{-6}}{L^3}$, where $W$ = weight in grams and $L$ = standard length in millimeters.

the monthly, annual, and local fluctuations in condition (the sexes followed the same trends in these fluctuations) and for the determination of the general length-weight curves.

The examination of the original tabulations failed to reveal detectable differences in the length-weight relationship of kiyis captured off different ports in the same general region of the lake (southern and northern central basins. northeastern island area). The question of differences between regions can be taken up best after the consideration of monthly and annual fluctuations (Table 15).

TABLE 15.—*Average coefficient of condition, K, according to year and season of capture, in different regions of Lake Michigan, with the data for the sexes combined*

[Number of specimens in parentheses]

| Month or months | Southern Lake Michigan | | Manistique | Northeastern island region |
|---|---|---|---|---|
| | 1930 | 1931 | 1932 | 1932 |
| May, June, July .............. | ........ | 1.35 | 1.39 | 1.30 |
| | ........ | (22) | (693) | (85) |
| August .......................... | 1.43 | 1.50 | ........ | 1.34 |
| | (801) | (584) | ........ | (245) |
| September .......................... | ........ | 1.58 | 1.45 | 1.26 |
| | ........ | (234) | (467) | (9) |
| October, November[1] ............ | 1.42 | 1.42 | ........ | ........ |
| | (22) | (1,534) | ........ | ........ |

[1]See Tables 17 and 18 for values of $K$ according to sex and state of organs during the spawning run. Spawning activities in 1931 were underway in late September but the fish of these collections were not weighed.

The best of the none too adequate data on monthly fluctuations in condition.[17] those for southern Lake Michigan in 1931. suggest an increase in the value of $K$ from the early season (May, June, and July; only 22 fish employed) through September. followed by a decline at the time of the spawning season (data for fish of all stages of maturity combined). Since figures were available in 1930 for August only it can not be stated whether or not $K$ increased during the late summer of that year. The $K$ of the October-November fish captured in 1930 (only 22 specimens; data combined without reference to state of organs of the fish) was only slightly smaller than that of fish taken in August. The data for the Manistique area in 1932 suggest an increase in $K$ from the early season to September similar (although less pronounced) to that which took place in southern Lake Michigan in 1931. In the northeastern island region, $K$ increased slightly in August but fell away in September (only nine fish in the September sample).

The 1930 and 1931 data provide the only available comparisons of

[17]Conclusions as to monthly, annual, and regional fluctuations in the length-weight relationship based on the average coefficient of condition are valid here since the changes of condition with length and the differences in the average lengths in the various collections both were small, and fish of all lengths showed similar variations in condition.

the condition of kiyis from the same region of the lake in different calendar years. The values of $K$ for the spawning-run fish were the same (1.42) in both years. There were relatively few fish, however, in the 1930 collection; furthermore, the values of $K$ of spawning-run samples are affected by the relative abundance of males and females and by the percentage of ripe or ripening and spent fish. Consequently, too great significance should not be assigned to this agreement. The more dependable August data indicate that kiyis were relatively heavier in 1931 ($K = 1.50$) than in 1930 ($K = 1.43$).

It would be difficult to state to what extent the differences between the $K$ values for 1931 and for the Manistique collections in 1932 represent annual fluctuation and to what extent they were the result of regional differences. In September the difference was large (1.58 in 1931; 1.45 in 1932). The data for August of 1930 and 1931 provide some evidence, however, that the condition of kiyis may have been somewhat above the average in the latter year. Further argument against the belief that the condition of kivis of the Manistique area normally differs greatly from that of kivis of southern Lake Michigan is provided by the fact that in the early season, contrary to the situation in September, the Manistique fish were relatively the heavier. In view of the preceding consideration it has been considered valid to determine a general length-weight curve based on the combination of the data for all collections for the great central basins of the lake.

The length-weight relationship was determined separately for kivis of the island region of northeastern Lake Michigan (about the Manitou, Fox, and Beaver Islands and neighboring reefs, and between these islands and the east shore), since the average values of $K$ for fish from this region were not only consistently lower than those for corresponding months in 1930 and 1931 but were also below the $K$ values for fish captured in the Manistique region in the same year (September comparison, however, based on few specimens from the island area). Possibly the comparatively poor condition of the kivis in the island region can be ascribed to the same unknown factors that caused the fish in the area to be relatively so sparse in comparison with the central basins of the lake (Hile and Deason, 1947).

The general length-weight data of Table 16 are presented graphically in Figure 3. The solid dots show the average weights of kivis from the great central basins of the lake by 5-millimeter intervals of standard length; the open dots give the corresponding information for fish from the island region of northeastern Lake Michigan. The smooth curves are the graphs of the following equations which were fitted to the data for those intervals represented by more than one specimen:

Central basins (upper curve)
$$W = 0.92404 \times 10^{-5} \, L^{3.077}.$$
Island region (lower curve)
$$W = 0.53314 \times 10^{-5} \, L^{3.167}.$$

TABLE 16.—*Relationship between the length and the weight of kiyis from the central basins of Lake Michigan, 1930-1932, and from the northeastern island region, 1932*

[The data for the sexes and for the various localities in each region have been combined. The lengths are the midpoints of 5-millimeter intervals of standard length.]

| Number of fish | Total length (inches) | Weight (ounces) | Standard length (millimeters) | Weight (grams) | K |
|---|---|---|---|---|---|
| | | Central | basins | | |
| 1 | 7.0 | 1.50 | 147 | 43 | 1.35 |
| .... | 7.5 | ...... | 157 | ...... | ...... |
| 1 | 7.8 | 2.00 | 162 | 57 | 1.34 |
| 1 | 8.0 | 2.50 | 167 | 71 | 1.52 |
| 6 | 8.2 | 2.25 | 172 | 64 | 1.26 |
| 2 | 8.5 | 2.25 | 177 | 64 | 1.15 |
| 9 | 8.7 | 3.02 | 182 | 86 | 1.43 |
| 25 | 9.0 | 3.39 | 187 | 96 | 1.47 |
| 73 | 9.2 | 3.59 | 192 | 102 | 1.44 |
| 118 | 9.4 | 3.88 | 197 | 110 | 1.44 |
| 272 | 9.7 | 4.30 | 202 | 122 | 1.48 |
| 377 | 9.9 | 4.61 | 207 | 131 | 1.48 |
| 604 | 10.2 | 4.95 | 212 | 140 | 1.47 |
| 599 | 10.4 | 5.25 | 217 | 149 | 1.46 |
| 763 | 10.6 | 5.53 | 222 | 157 | 1.43 |
| 514 | 10.8 | 5.84 | 227 | 166 | 1.42 |
| 448 | 11.0 | 6.18 | 232 | 175 | 1.40 |
| 225 | 11.3 | 6.50 | 237 | 184 | 1.38 |
| 176 | 11.5 | 6.91 | 242 | 196 | 1.38 |
| 79 | 11.8 | 7.32 | 247 | 208 | 1.38 |
| 46 | 12.0 | 7.66 | 252 | 217 | 1.36 |
| 10 | 12.2 | 8.05 | 257 | 228 | 1.34 |
| 3 | 12.5 | 8.87 | 262 | 251 | 1.40 |
| 2 | 12.7 | 9.50 | 267 | 269 | 1.41 |
| .... | 12.9 | ...... | 272 | ...... | ...... |
| 2 | 13.2 | 10.70 | 277 | 303 | 1.43 |
| 1 | 13.7 | 11.70 | 287 | 332 | 1.40 |
| | | Island | region | | |
| .... | 7.0 | ...... | 147 | ...... | ...... |
| 1 | 7.5 | 2.00 | 157 | 57 | 1.45 |
| .... | 7.8 | ...... | 162 | ...... | ...... |
| .... | 8.0 | ...... | 167 | ...... | ...... |
| 1 | 8.2 | 1.75 | 172 | 50 | 0..8 |
| 1 | 8.5 | 2.25 | 177 | 64 | 1.15 |
| 1 | 8.7 | 3.50 | 182 | 99 | 1.64 |
| 1 | 9.0 | 3.00 | 187 | 85 | 1.30 |
| 1 | 9.2 | 3.00 | 192 | 85 | 1.20 |
| 11 | 9.4 | 3.32 | 197 | 94 | 1.23 |
| 9 | 9.7 | 3.58 | 202 | 101 | 1.23 |
| 13 | 9.9 | 4.21 | 207_ | 119 | 1.34 |
| 20 | 10.2 | 4.59 | 212 | 130 | 1.:6 |
| 30 | 10.4 | 4.95 | 217 | 140 | 1.37 |
| 47 | 10.6 | 5.17 | 222 | 147 | 1.34 |
| 49 | 10.8 | 5.55 | 227 | 157 | 1.34 |
| 45 | 11.0 | 5.94 | 232 | 168 | 1.35 |
| 39 | 11.3 | 6.09 | 237 | 173 | 1.30 |
| 33 | 11.5 | 6.49 | 242 | 184 | 1.30 |
| 15 | 11.8 | 6.83 | 247 | 194 | 1.29 |
| 13 | 12.0 | 7.75 | 252 | 220 | 1.37 |
| 6 | 12.2 | 7.80 | 257 | 221 | 1.30 |
| 3 | 12.5 | 8.75 | 262 | 248 | 1.38 |
| .... | 12.7 | ...... | 267 | ...... | ...... |
| 1 | 12.9 | 10.25 | 272 | 291 | 1.45 |
| .... | 13.2 | ...... | 277 | ...... | ...... |
| .... | 13.7 | ...... | 287 | ...... | ...... |

In both equations $W$ = weight in grams and $L$ = standard length in millimeters.

The examination of the position of the dots in Figure 3 with respect to the curves reveals only a moderately good agreement between the
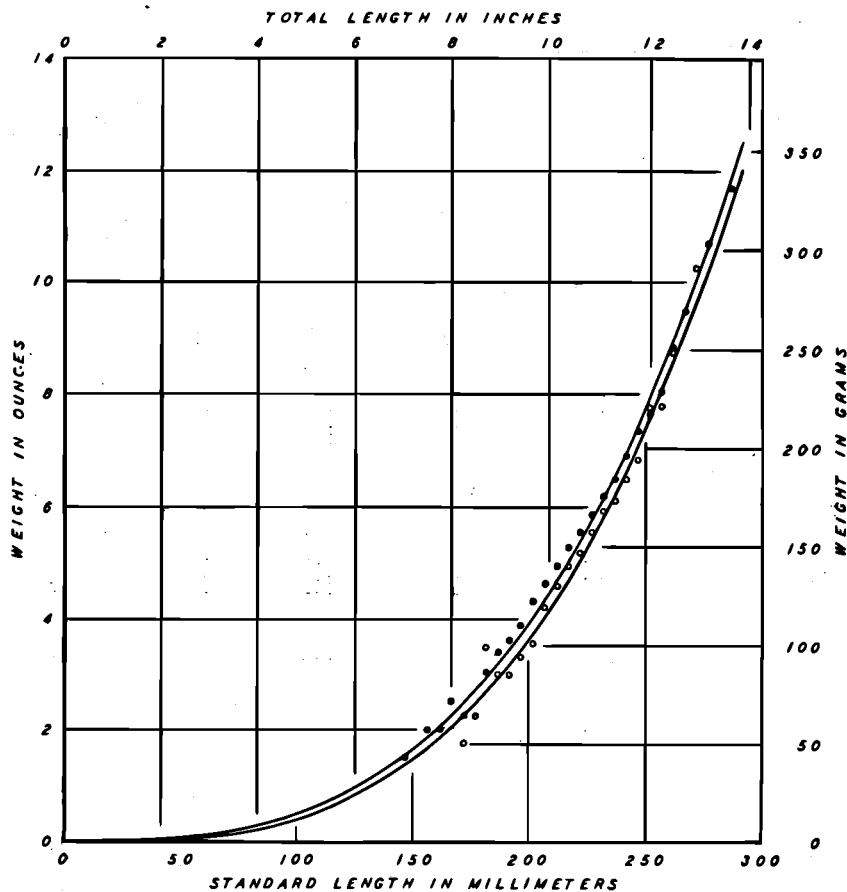
FIGURE 3.—Length-weight relationship of the kiyi in the central basins of Lake Michigan (upper curve and solid dots) and in the northeastern island region (lower curve and open dots). The dots represent the empirical data; the smooth curves are graphs of the equations given in the text.

empirical and theoretical weights. The largest discrepancies, to be sure, are to be found at intervals represented by relatively few fish. On the other hand, disagreements that were consistently in the same direction over fairly large intervals occurred at lengths that were extremely well represented. For example, the actual weights of kiyis from the central basins exceeded the computed weights at every length from 182 millimeters to 227 millimeters, inclusive, although the aver-

ages of 9 of the 10 length intervals were based on 25 fish or more and 7 intervals were represented by more than 100 specimens. In the interval, 237-267 millimeters, the actual weights were consistently lower than the theoretical weights (5 of 7 lengths with 10 fish or more and 2 with more than 100 specimens). The length-weight data for kiyis of the northeastern island region likewise exhibited discrepancies that were consistently in the same direction over considerable intervals of length.

Extremely close agreement between actual and computed weights should not be expected since the empirical values were derived from a combination of all available data regardless of sex, state of organs, or month or year (in the central basins) of capture. Differences traceable to one of these factors together with some variation from sample to sample in the length-frequency distribution of the kiyis doubtless brought about part of the irregularities detectable in the empirical data. Gill-net selection according to condition (see p. 131) also may have played an important role. In view of the logical explanations for the discrepancies between the observed and calculated weights, it may be concluded that the equations may be employed legitimately for the purpose for which they were derived, that of expressing the general length-weight relationship of the kiyi in the two regions of Lake Michigan.

The values of the exponent $n$ in the two equations show that for the collections as a whole the weight of the kiyis increased to a power slightly greater than the cube of the length both in the central basins of Lake Michigan ($n = 3.077$) and in the northeastern island region ($n = 3.167$). When $n > 3$ the coefficient of condition $K$ may be expected to increase with increase in the length of the fish. (This increase in $K$ is to the $n-3$ power of the length.) The actual values of $K$ in Table 16, however, show an extremely irregular variation of the coefficient. These irregularities correspond to the discrepancies between the actual and calculated weights discussed in earlier paragraphs.

In the central basins, 75.9 per cent of all kiyis weighed fell within the size range bounded by the average weights of 4.61 and 6.18 ounces (corresponding total lengths, 9.9 and 11.0 inches). The bulk (71.7 per cent) of the kiyis from the island region were within the interval bounded by the average weights of 4.95 and 6.49 ounces (corresponding total lengths, 10.4 and 11.5 inches). The grand average weights were 5.43 ounces (154 grams) in the central basins and 5.58 ounces (158 grams) in the northeastern islands. The higher average for fish from the island region can be traced to their greater average length— 10.8 inches (227 millimeters) as compared with 10.5 inches (220 millimeters) for kiyis from the central basins.

*Loss of weight at spawning.*—Records of the length and weight of ripe or nearly ripe and spent kiyis of the 1931 spawning run have

made possible a study of the loss of weight at spawning of both males (Table 17) and females (Table 18).[18]

The loss of weight of male kiyis was altogether unimportant. Two of 13 comparisons of fish of the same length interval actually indicated an increase of weight, 2 showed no change, and 9 showed losses that ranged from 0.7 to 7.4 per cent. The mean percentage loss[19] was 1.6.

The loss of weight of female kiyis at spawning was considerable. Every comparison indicated a decrease, with the percentages ranging from 6.2 to 14.4. The variation of these percentages with length exhibited no clear-cut trend although apparently the highest values were at the intermediate lengths. The weighted mean percentage loss was 11.8. Female kiyis, therefore, lost between one eighth and one ninth of their weight at spawning. This estimate should be recognized as minimal, since some individuals designated as ripe may have shed some of their eggs and others listed as spent may still have retained a few.

Comparisons of the grand average values of $K$ in Tables 17 and 18 with those of Table 15 reveal that in 1931 the coefficient of condition was lower among all categories of spawning-run fish, including even the ripe and nearly ripe females, than it was in August and early September before the onset of spawning (these latter averages were based on a combination of the sexes; sex differences were small, however,—see p. 122). The relatively low value of $K$ for the ripe and nearly ripe females is particularly striking since it runs counter to the commonly held belief that fish attain their maximum weight just before spawning. Apparently the weight of kiyis declines from August and early September to the spawning period. At the time the sex products are discharged further loss of weight occurs (large for the females; small for the males).

*Effect of gill-net selection on the estimation of the value of the coefficient of condition.*—Although numerous investigations have been carried out on the relationship between the size of gill-net meshes and the number and average size of the fish captured, little attention has been given the effect of gill-net selection on the estimation of the value of the coefficient of condition, $K$. A fairly detailed treatment of this question was made, however, by Farran (1936) who studied the relationship between the $K$ values of marine herring and the size of mesh in drift nets. Farran observed that "the greatest girth of herrings

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[18]The data of Tables 17 and 18 were obtained from collections in Wisconsin taken off Kewaunee on October 5 and 15 and November 5, off Sheboygan on November 6, and off Racine on October 9 and 30. The data for certain small, scattered collections and for certain earlier collections that contained few or no spent fish (the category for which information was least plentiful) were not tabulated. The combination of the materials for different localities was made only after the examination of the data proved the procedure to be valid.

[19]In the computation of the mean, each percentage loss was weighted by the product of the number of ripe or nearly ripe and spent individuals involved in the comparison. For example, the first percentage (—8.2) was given a weight, $2 \times 7 = 14$; the second percentage had the weight $6 \times 6 = 36$; . . . .

TABLE 17.—*Comparison of the weights of spent male kiyis of the 1931 spawning run with those of ripe and nearly ripe males of the same length*

[The total lengths are equivalent to the midpoints of the intervals of standard length. See footnote 19 for method of computing the average percentage loss]

| Standard length (millimeters) | Total length (inches) | Ripe or nearly ripe | | | Spent | | | Loss at spawning | Percentage loss |
|---|---|---|---|---|---|---|---|---|---|
| | | Number of fish | Weight (grams) | K | Number of fish | Weight (grams) | K | | |
| 185-189 | 9.0 | 2 | 85 | 1.30 | 7 | 92 | 1.41 | —7 | —8.2 |
| 190-194 | 9.2 | 6 | 103 | 1.46 | 6 | 101 | 1.43 | 2 | 1.9 |
| 195-199 | 9.4 | 17 | 109 | 1.43 | 11 | 109 | 1.43 | 0 | 0.0 |
| 200-204 | 9.7 | 20 | 115 | 1.40 | 21 | 111 | 1.35 | 4 | 3.5 |
| 205-209 | 9.9 | 42 | 123 | 1.39 | 23 | 123 | 1.39 | 0 | 0.0 |
| 210-214 | 10.2 | 45 | 135 | 1.42 | 26 | 133 | 1.40 | 2 | 1.5 |
| 215-219 | 10.4 | 30 | 137 | 1.34 | 17 | 132 | 1.29 | 5 | 3.6 |
| 220-224 | 10.6 | 29 | 147 | 1.34 | 12 | 143 | 1.31 | 4 | 2.7 |
| 225-229 | 10.8 | 15 | 153 | 1.31 | 10 | 152 | 1.30 | 1 | 0.7 |
| 230-234 | 11.0 | 9 | 167 | 1.34 | 6 | 158 | 1.27 | 9 | 5.4 |
| 235-239 | 11.3 | 1 | 176 | 1.32 | 2 | 163 | 1.22 | 13 | 7.4 |
| 240-244 | 11.5 | 3 | 175 | 1.23 | 1 | 190 | 1.34 | —15 | —8.6 |
| 245-249 | 11.8 | 2 | 188 | 1.25 | 2 | 180 | 1.19 | 8 | 4.3 |
| 250-254 | 12.0 | 3 | 191 | 1.19 | ..... | ..... | ..... | ..... | ..... |
| 275-279 | 13.2 | 1 | 278 | 1.31 | ..... | ..... | ..... | ..... | ..... |
| 285-289 | 13.7 | ..... | ..... | ..... | 1 | 332 | 1.40 | ..... | ..... |
| Total or average | | 225 | ..... | 1.37 | 145 | ..... | 1.36 | ..... | 1.6 |

TABLE 18.—*Comparison of the weights of spent female female kiyis of the 1931 spawning run with those of ripe and nearly ripe females of the same length*

[The total lengths are equivalent to the midpoints of the intervals of standard length. See footnote 19 for method of computing the average percentage loss]

| Standard length (millimeters) | Total length (inches) | Ripe or nearly ripe | | | Spent | | | Loss at spawning | Percentage loss |
|---|---|---|---|---|---|---|---|---|---|
| | | Number of fish | Weight (grams) | K | Number of fish | Weight (grams) | K | | |
| 170-174 | 8.2 | 1 | 48 | 0.94 | ..... | ..... | ..... | ..... | ..... |
| 180-184 | 8.7 | 2 | 89 | 1.48 | ..... | ..... | ..... | ..... | ..... |
| 185-189 | 9.0 | 1 | 96 | 1.47 | 3 | 96 | 1.36 | 11 | 10.3 |
| 190-194 | 9.2 | 10 | 107 | 1.51 | 7 | 105 | 1.37 | 7 | 6.2 |
| 195-199 | 9.4 | 19 | 112 | 1.46 | 22 | 116 | 1.41 | 10 | 7.9 |
| 200-204 | 9.7 | 55 | 126 | 1.53 | 32 | 122 | 1.38 | 15 | 10.9 |
| 205-209 | 9.9 | 88 | 137 | 1.54 | 47 | 126 | 1.32 | 19 | 13.1 |
| 210-214 | 10.2 | 137 | 145 | 1.52 | 35 | 134 | 1.31 | 18 | 11.8 |
| 215-219 | 10.4 | 141 | 152 | 1.49 | 40 | 141 | 1.29 | 19 | 11.9 |
| 220-224 | 10.6 | 175 | 160 | 1.46 | 28 | 148 | 1.27 | 18 | 10.8 |
| 225-229 | 10.8 | 100 | 166 | 1.42 | 26 | 152 | 1.22 | 23 | 13.1 |
| 230-234 | 11.0 | 71 | 175 | 1.40 | 15 | 169 | 1.27 | 19 | 10.1 |
| 235-239 | 11.3 | 41 | 188 | 1.41 | 7 | 166 | 1.17 | 28 | 14.4 |
| 240-244 | 11.5 | 29 | 194 | 1.37 | 6 | 192 | 1.27 | 20 | 9.4 |
| 245-249 | 11.8 | 11 | 212 | 1.41 | 1 | 204 | 1.27 | 14 | 6.4 |
| 250-254 | 12.0 | 5 | 218 | 1.36 | ..... | ..... | ..... | ..... | ..... |
| 255-259 | 12.2 | 3 | 198 | 1.17 | ..... | ..... | ..... | ..... | ..... |
| 260-264 | 12.5 | 1 | 281 | 1.56 | ..... | ..... | ..... | ..... | ..... |
| 275-279 | 13.2 | 1 | 329 | 1.55 | ..... | ..... | ..... | ..... | ..... |
| Total or average | | 891 | ..... | 1.47 | 269 | ..... | 1.31 | ..... | 11.8 |

and the girth behind the gill cover . . . are proportional to the condition factor, $K$, . . . .'', and concluded therefore, '' . . . . that the catching power of a net is dependent on the condition of the fish as well as on the length.'' It follows that the shorter fish captured by a net of a particular mesh size should be the individuals with the greater relative girth (and hence, the higher values of $K$) whereas the longer fish taken in the same mesh should be those with the smaller relative girth (and the lower values of $K$). Furthermore, fish of the same length captured in nets of successively larger meshes should have successively greater average values of $K$.

The effect of gill-net selection on the $K$ of the kivi was studied for the IV-group females of the Port Washington, Wisconsin, collection. Not only did this sample have the advantage of homogeneity as to age, sex, and maturity (all mature) but all fish were captured off the same port within a relatively short period of time (the dates of collection were August 13 and 21, 1931). The expected relationships outlined at the end of the preceding paragraph are met by the data of Table 19, for the values of $K$ did tend to decrease with increase in

TABLE 19.—*Variation of the coefficient of condition,* K, *of the IV-group female kiyis of the Port Washington collection according to length and to the size of mesh of the gill nets by which they were captured*

[Numbers of specimens in parentheses]

| Standard length (millimeters) | Mesh (extension measure in inches) | | | | | Average |
|---|---|---|---|---|---|---|
| | 2⅜ | 2½ | 2⅝ | 2¾ | 3 | |
| 190-194 | ...... | 1.46 (1) | ...... | ...... | ...... | 1.46 (1) |
| 195-199 | 1.60 (1) | ...... | 1.35 (1) | ...... | ...... | 1.48 (2) |
| 200-204 | 1.56 (10) | 1.64 (6) | 1.90 (2) | 1.72 (2) | ...... | 1.63 (20) |
| 205-209 | 1.53 (22) | 1.64 (8) | 1.72 (3) | 1.32 (1) | 1.25 (1) | 1.56 (35) |
| 210-214 | 1.50 (26) | 1.57 (15) | 1.66 (6) | 1.60 (6) | 1.49 (1) | 1.55 (54) |
| 215-219 | 1.48 (28) | 1.53 (15) | 1.57 (15) | 1.58 (5) | 1.82 (1) | 1.53 (64) |
| 220-224 | 1.42 (20) | 1.46 (16) | 1.56 (12) | 1.55 (4) | 1.62 (1) | 1.48 (53) |
| 225-229 | 1.48 (5) | 1.49 (7) | 1.45 (4) | 1.56 (8) | 1.40 (1) | 1.50 (25) |
| 230-234 | 1.28 (2) | 1.50 (2) | 1.49 (2) | 1.50 (5) | ...... | 1.46 (11) |
| 235-239 | ...... | ...... | 1.49 (1) | ...... | ...... | 1.49 (1) |
| 240-245 | ...... | 1.74 (1) | ...... | ...... | ...... | 1.74 (1) |
| Average $K$ | 1.49 | 1.54 | 1.58 | 1.56 | 1.52 | 1.53 |
| Average length | 214 (114) | 215 (71) | 217 (46) | 220 (31) | 216 (5) | 216 (267) |

length among fish captured in the same net and to increase with increase in mesh size among fish of the same length taken by nets of different mesh. There were, it is true, certain exceptions to the general trends, but relatively few fish were involved. Not only were the numbers of fish too small at certain lengths and for certain meshes to yield reliable averages for $K$, but it is possible also that some of the fish in the poorly represented groups were not caught by the body in the typical manner. The smallest and largest individuals captured by a gill net of a particular mesh size frequently are "accidental" captures, that is, are fish that have become tangled in the meshes by the mouth parts. These fish would not, of course, be subjected to the same selection with respect to condition as those held by the body.

Computations of the average increase of $K$ per 5-millimeter increase in length of fish taken in the same nets and of the increase of $K$ per ⅛-inch increase in mesh size among fish of the same length interval provide a measure of the selective action of nets with respect to condition. In the calculation of these averages each change of $K$ was weighted by the product of the number of fish in each of the two groups compared. (See footnote 19.)

The mean, computed by this procedure, indicated that with kiyis captured by nets of the same mesh the value of $K$ decreased 0.034 for each 5-millimeter increase in length. It cannot be stated, however, that this decrease was entirely the result of gill-net selection, for the combined samples of all nets (extreme right of Table 19) also exhibited a decrease in $K$ with increase in length (0.026 per 5 millimeters). This latter decline suggests that a drop in $K$ with greater length, independent of gill-net selection, may be characteristic of the fish from which the sample was drawn. On the other hand, if it could be assumed that none of the five mesh sizes employed was able to capture the slender individuals among the shorter IV-group females from Port Washington, the decrease in $K$ in the complete sample as well as in the samples for the individual nets might be attributed to gillnet selection. At any rate, it should be noted that the decline of $K$ with increase in body length was greater in samples of fish caught by nets of the same mesh size than in the combined samples of all nets.

The strongest evidence for a pronounced selective action of gill nets with respect to the coefficient of condition is to be found in the data on the average $K$ of fish of the same length interval captured in nets of different mesh size, since the relation of $K$ to length in the entire sample has no bearing on the significance of these comparisons. For fish of the same length, each ⅛-inch increase in the mesh size of the gill nets was accompanied by an average increase of 0.057 in the value of $K$. This change amounts to 3.7 per cent of the grand average $K$ value of 1.53 for the entire age group.

Comparisons between nets with all lengths of fish combined revealed a smaller increase (0.039) per ⅛-inch increase in mesh size. This smaller increase no doubt can be explained by the tendency for the

nets with successively larger meshes to take fish with greater average lengths. When length increases with increase in mesh size a smaller increase in the relative girth (and hence in condition) is to be expected than when comparisons are limited to fish of the same length.

The data just discussed suggest the advisability of considerable caution in the use of length-weight data from gill-net samples. Since the value of $K$ for fish taken by a particular net is influenced by the size range of the fish available, and since the average $K$ of samples of fish of a particular size is affected by the sizes of gill-net mesh fished, it is obvious that differences in the average values of $K$ in samples from stocks with different size distributions and/or taken by nets of different mesh size may be the result of gear selection and hence in no way reflect true differences in the nature of the populations from which the samples were drawn.

## MATURITY

The kiyi matures at a small size. Mature females were found down to a standard length of 143 millimeters or a total length of 6.8 inches and mature males down to a length of 146 millimeters or 7.0 inches (no smaller fish were examined). Koelz (1929) made no statement as to the size at maturity of the Lake Michigan or Lake Huron kiyis; in Lake Superior and Lake Ontario, however, the smallest specimens (132 and 148 millimeters, standard length, respectively) were found to be mature.

Only 11 Lake Michigan kiyis of the more than 6,000 examined were immature. Their immaturity was not related to small size for their standard length (10 fish measured) averaged 226 millimeters (total length, 10.8 inches) and ranged from 199 to 258 millimeters (9.5 to 12.3 inches). Inasmuch as these "immature" kiyis averaged as long or longer than fish in the general samples (Table 6) it probably would be more suitable to term them "non-functional." Their presence suggests that "adult" fish occasionally may fail to spawn.

## SEX RATIO

The collections of kiyis from Lake Michigan were characterized at all times by a strong preponderance of females (Table 20). The dominance of the females was less pronounced, however, in the spawning-run collections (75.2 per cent of the total) than in late-spring, summer, and early-autumn samples (90.2 per cent of the total).

*Sex ratio in summer collections.*—The data give no conclusive evidence for a significant monthly fluctuation of the sex ratio over the period, May to mid-September. In 1930 the relative abundance of the sexes was practically the same in July and August, the two months for which data were available. Males appear to have been more plentiful in May, June, and July in 1931 than in August and early September. In 1932 the monthly changes in the sex ratio were irregular. The greatest relative abundance of males in 1932 occurred in June and August and the lowest in July and September. In this last month

TABLE 20.—*Numbers and percentages (in parentheses) of males and females in the kiyi collections of different months, 1930-1932*

| Month | 1930 | | 1931 | | 1932 | | 1930-1932 | |
|---|---|---|---|---|---|---|---|---|
| | Males | Females | Males | Females | Males | Females | Males | Females |
| May .......................... | ...... | ...... | 16 (16.7) | 80 (83.3) | ...... | ...... | 16 (16.7) | 80 (83.3) |
| June ...................... | ...... | ...... | 16 (13.6) | 102 (86.4) | 16 (7.3) | 202 (92.7) | 32 (9.5) | 304 (90.5) |
| July .......................... | 53 (12.0) | 389 (88.0) | 12 (23.5) | 39 (76.5) | 38 (6.8) | 524 (93.2) | 103 (9.8) | 952 (90.2) |
| August ................... | 144 (12.8) | 985 (87.2) | 95 (9.1) | 949 (90.9) | 22 (8.7) | 230 (91.3) | 261 (10.8) | 2,164 (89.2) |
| September (first half) ................... | ...... | ...... | 23 (10.1) | 205 (89.9) | 18 (3.8) | 454 (96.2) | 41 (5.9) | 659 (94.1) |
| Total ................... | 197 (12.5) | 1,374 (87.5) | 162 (10.5) | 1,375 (89.5) | 94 (6.2) | 1,410 (93.8) | 453 (9.8) | 4,159 (90.2) |
| Mid-September to mid-November .... | 6 (25.0) | 18 (75.0) | 592 (24.7) | 1,800 (75.3) | ...... | ...... | 598 (24.8) | 1,818 (75.2) |

males were extremely scarce—only 3.8 per cent of the total. The monthly fluctuations in the combined 1930-1932 collections (right of table) have little significance as they are affected too greatly by annual fluctuations in the ratio in combination with differences in the representation of the individual months.

The totals for the "summer" (May to mid-September) collections show a decrease in the percentage of males from 12.5 in 1930 to 10.5 in 1931 and 6.2 in 1932. The difference between 1930 and 1931 was not large. The 1932 percentage, however, was extremely low.

The relationship between the size of the gill-net meshes and the sex ratio of the kiyis captured was investigated in an attempt to learn whether gear selection may account for the small percentage of males in the 1932 samples in comparison with the percentages in 1930 and 1931 and also for the relatively small representation of males in the collections as a whole. This possibility was suggested by the fact that 1932, which was the only year in which 2⅜- and 3-inch-mesh nets were not fished, was also the year in which the percentage of males was lowest.

In view of the slower growth and somewhat more slender form of the males as compared with the females, it might logically be expected that the percentage of males in samples of this small chub should decrease with increase in the mesh size of the gill nets with which the fish were captured. The possibility was considered also that most or all of the mesh sizes in the experimental gill nets might be too large to sample the males as satisfactorily as females and hence that the general scarcity of males in the collections might not reflect at all the relative abundance of the sexes in the population. The data of Table 21, however, fail to reveal a clear-cut relationship between mesh size and the relative abundance of the sexes in samples of kiyis.

TABLE 21.—*Relationship between the mesh size (extension measure in inches) of gill nets and the sex ratio of the kiyis taken*

| Year and season | Item | Gill-net mesh | | | | |
|---|---|---|---|---|---|---|
| | | 2 ⅜ | 2 ½ | 2 ⅝ | 2 ¾ | 3 |
| 1930 (Summer) | Number of males ...................... | 104 | 42 | 32 | 4 | 15 |
| | Number of females .................... | 828 | 284 | 138 | 83 | 41 |
| | Percentage males ...................... | 11.2 | 12.9 | 18.8 | 4.6 | 26.8 |
| 1931 (Summer) | Number of males ...................... | 88 | 38 | 20 | 9 | 7 |
| | Number of females .................... | 539 | 441 | 229 | 121 | 45 |
| | Percentage males ...................... | 14.0 | 7.9 | 8.0 | 6.9 | 13.5 |
| 1932 (Summer) | Number of males ...................... | .... | 54 | 31 | 9 | .... |
| | Number of females .................... | .... | 808 | 427 | 175 | .... |
| | Percentage males ...................... | .... | 6.3 | 6.8 | 4.9 | .... |
| 1931 (Spawning period)[1] | Number of males ...................... | 417 | 119 | 38 | 10 | 7 |
| | Number of females .................... | 794 | 521 | 344 | 121 | 18 |
| | Percentage males ...................... | 34.4 | 18.6 | 9.9 | 7.6 | 28.0 |

[1]One male and two females from a special experimental net were omitted.

In both of the 1931 series of samples the 2⅜-inch-mesh net took a much higher percentage of males than did nets of the next three higher mesh sizes and the trend was toward a lesser relative abundance of males as the mesh size increased. (See two paragraphs later for a discussion of the data for the 3-inch-mesh nets.) In 1930, on the other hand, the percentage of males increased with increase in mesh size from 2⅜ to 2⅝ inches; males were extremely scarce, however, in the samples from the 2¾-inch net. The percentage of males did not vary widely in the samples from the three mesh sizes fished in 1932. The lowest percentage was from the largest mesh, but the smallest mesh did not have the highest percentage.

The data for these same four (or three) mesh sizes indicate also that the percentage of males varied considerably from year to year in samples from the same net. The range of variation (summer collection) was: 11.2-14.0 for the 2⅜-inch-mesh nets (only two years); 6.3-12.9 for the 2½-inch mesh; . . . . These annual differences are of the same general order of magnitude as the differences among the various mesh sizes in the same year.

The figures for the 3-inch-mesh net were omitted from the discussion of the preceding paragraph as not comparable to those for the nets of smaller mesh. Considerable numbers of the fish taken by nets of this mesh are known (from direct observation supported by the examination of the records) to have consisted of small individuals whose mouth parts had become entangled in the webbing. These small fish, which were not caught in the customary manner by gilling, were not subject to the type of selection with which the discussion of the previous paragraphs was concerned. The high percentages suggest that many of them were males. Because of these consistently high percentages the elimination of the 3-inch-mesh net from the experimental series in 1932 very likely had some influence on the determination of the sex ratio in that year. This effect probably was not large as the number of kiyis captured by the 3-inch-mesh nets in earlier years was always small in comparison with the catch of other nets.

The lack of a consistent trend in the fluctuations of the sex ratio of samples of kiyis from nets of successively larger mesh and the rather large variation from year to year in the percentage of males in samples from nets of the same mesh size leave in doubt the effect of gear selection on the value of the ratio. It is possible, indeed probable, that net selection contributed to the low percentage of males in the 1932 collection (in comparison with summer collections of other years) and also to the generally low percentages of males in the samples of kiyis. The available data fail entirely, however, to indicate how extensive this selection might have been.

Differences in the age composition of the samples from different areas of Lake Michigan also may account in part for the fact that the 1932 samples contained relatively fewer males than did the 1930 and 1931 collections. It was brought out earlier (p. 93) that the average age of kiyis was lower in southern Lake Michigan (the region from which the 1930 and 1931 samples were obtained) than in northern Lake Michigan (the scene of the 1932 fishing). Since, as will be shown later in this section, the relative abundance of males tends to decrease with increase in the age of summer-caught kiyis, the scarcity of males in the 1932 samples well may be partly the result of the relatively high average age of the stock in the region in which the collections were made.

The combined possible distorting effects of gear selection and of differences in the age of fish in the samples make it impossible to conclude that the low percentage of males in the 1932 collections reflects a true regional difference in the sex ratio of kiyis taken in summer.

*Sex ratio in spawning-run collections.*—The available evidence (Table 20) indicates that, as is frequently true among fish, male kiyis are taken more plentifully during the spawning run than at any other period. The relative abundance of males was more than twice as great in the spawning-run samples as in the summer collections of 1931, the only year in which large numbers of fish were collected in both periods. (The numbers of fish taken during the 1930 spawning-run were inadequate, and the close agreement with 1931 with respect to the percentage of males should be considered strictly a coincidence.)

The cause of the greater percentage of males in the spawning-run samples is largely a matter for speculation. A plausible explanation is that based on the assumption that the activity of the males increases greatly during the spawning period. Since the catch of stationary gear is a function both of the number of fish present at a size subject to capture and of their movements, it follows that if the activity of the members of one sex is increased more than that of the other, the percentage representation of the sexes in the catch will be changed even though the relative abundance of males and females on the grounds is not altered.

The high percentage of males in the spawning-run collections of various species frequently has been explained as the result of the ten-

dency for fish of that sex to arrive on the spawning grounds earlier and remain there longer than do the females. This explanation does not appear to be acceptable for the kiyi. The assumption that males are on the spawning grounds in numbers out of proportion to their true abundance in the population carries with it the tacit implication that there exists somewhere a residue of the stock in which males are correspondingly scarce. All the fishing operations during the 1931 spawning season of the kiyi, however, failed to discover this hypothetical portion of the population. Although the sex ratio of samples taken during the spawning period did vary from day to day (Hile and Deason, 1947) the percentages of males were uniformly above the average for the summer samples. It should be emphasized that the operations with experimental gill nets were part of an investigation of all shubs and were not carried out with special reference to the kiyi. The various depths and localities from about 20 fathoms to 90 fathoms were covered with sufficient thoroughness that it is hardly conceivable that portions of the kiyis stock that contained almost no males would not have been found. It is possible, of course, that aggregations of kiyis in which the fish were almost exclusively females may have been present at greater depths than were fished.

It is conceivable also that during the summer a greater proportion of the males than of the females were living somewhat above the bottom beyond the reach of gill nets (which rested on the bottom and were only 5 feet deep) or at greater depths than were fished, whereas during the spawning period the availability of the sexes may have been equal or more nearly equal. In such a situation, barring further complicating effects of a seasonal differential activity of the sexes, the relative numbers of males and females in the catch might reflect their true proportions at the levels and on the grounds fished but not necessarily in the entire population. There is no evidence, however, for such a difference in the distribution of the sexes; in fact, nothing is known of the extent to which fish of either sex may live sufficiently far above the bottom to escape capture by gill nets.

The lack of good evidence as to the validity of any of the preceding explanations forces the general conclusion that the cause of the increase in the abundance of male kiyis in the catch during the spawning season is at yet unknown.

*Changes in sex ratio with increase in age.*—For the presentation of the data on the variation of the sex ratio with age (Table 22) the order of arrangement of the ports has been varied from that employed in earlier tables. This change has been made to facilitate the comparison of the information for the summer collections (northern Lake Michigan and Port Washington) and the spawning-run samples (Kewaunee and Racine).

The percentage of males decreased rather consistently with the increase in age in the summer collections (exception provided by age-group IV from northern Lake Michigan) through age-group VI or

TABLE 22.—*Representation of the sexes in the age groups of the kiyi collections.*

[Samples were obtained from northern Lake Michigan and off Port Washington during the summer; collections off Kewaunee and Racine were from the spawning run (October)]

| Locality | Item | Age group | | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|
| | | II | III | IV | V | VI | VII | VIII | X | |
| Northern Lake Michigan[1] | Number of males | 1 | 1 | 8 | 15 | 8 | 1 | … | … | 34 |
| | Number of females | … | 15 | 77 | 260 | 153 | 40 | 4 | 1 | 551 |
| | Percentage of males | 50.0 | 6.2 | 9.4 | 5.5 | 5.0 | 2.4 | 0.0 | 0.0 | 5.8 |
| Port Washington, Wisconsin | Number of males | 1 | 6 | 23 | 9 | 1 | 2 | 1 | … | 40 |
| | Number of females | … | 27 | 267 | 138 | 20 | … | … | … | 455 |
| | Percentage of males | 100.0 | 18.2 | 7.9 | 6.1 | 4.8 | 0.0 | 0.0 | … | 8.1 |
| Kewaunee, Wisconsin | Number of males | 1 | 19 | 20 | 12 | 1 | … | … | … | 53 |
| | Number of females | 3 | 49 | 130 | 63 | 14 | … | 1 | … | 260 |
| | Percentage of males | 25.0 | 27.9 | 13.3 | 16.0 | 6.7 | … | 0.0 | … | 16.9 |
| Racine, Wisconsin | Number of males | 4 | 11 | 20 | 8 | 1 | 1 | … | … | 45 |
| | Number of females | 22 | 63 | 95 | 25 | 5 | 1 | … | … | 211 |
| | Percentage of males | 15.4 | 14.9 | 17.4 | 24.2 | 16.7 | 50.0 | … | … | 17.8 |
| Northern Lake Michigan and Port Washington | Number of males | 2 | 7 | 31 | 24 | 9 | 1 | … | 1 | 74 |
| | Number of females | 1 | 42 | 344 | 398 | 173 | 42 | 5 | … | 1,006 |
| | Percentage of males | 66.7 | 14.3 | 8.3 | 5.7 | 4.9 | 2.3 | 0.0 | 0.0 | 6.9 |
| Kewaunee and Racine | Number of males | 5 | 30 | 40 | 20 | 2 | 1 | … | … | 98 |
| | Number of females | 25 | 112 | 225 | 88 | 19 | 1 | 1 | … | 471 |
| | Percentage of males | 16.7 | 21.1 | 15.1 | 18.5 | 9.5 | 50.0 | 0.0 | … | 17.2 |

[1]Combined Manistique and Fox Islands collections from State of Michigan waters.

VII beyond which age no males at all were taken. In the combined summer collections the percentage of males declined consistently from the II group to the VII group. The six older fish were all females.

In spawning-run fish from Kewaunee also the relative abundance of the males tended to decrease with increase in age. At Racine, however, the trend was toward an increase in the percentage of males at the higher ages. No trend toward a change of the sex ratio can be discovered in the data for the combined spawning-run samples. The equal relative abundance of males among young and old spawning-run fish is brought out by the fact that members of this sex made up 17.2 per cent of the total number of fish in age-groups II to IV and 17.4 per cent of the individuals older than the IV group.

Of the three conditions, decrease (summer and Kewaunee spawning-run collections), increase (Racine collection), or no change (combined spawning-run collections) in the relative abundance of males with increase in age, the first appears to be the most likely to represent the true trend within the population. Not only did three of four collections (the one from northern Lake Michigan consisted of a combination of four samples) exhibit a tendency toward a decrease in the percentage of males with advancing age, but this type of change is the same that has been observed repeatedly for other species and seems to be common among fish. Furthermore, too great significance should not be given to the exception provided by the Racine collection since the sex ratio is known frequently to be abnormal in spawning-run samples. It may be concluded, therefore, that a decline in the relative abundance of males with increasing age is normal for the Lake Michigan kiyi.

It should be pointed out that the decrease in the percentage of males with increase in age cannot be ascribed logically to gear selection and hence considered an apparent rather than a real phenomenon. The possibility was mentioned earlier in this section that the relatively slowly growing and slender males might have been sampled by the experimental nets less efficiently than females and therefore that gear selection might have contributed to the general scarcity of males in the samples. A selection of this type, however, should tend to cause the relative abundance of the males to increase rather than to decrease with age since the greater size of the older males should permit them to be captured more easily than the younger males.

A progressive decline with increasing age in the relative abundance of males can be explained best on the basis of differential mortality of the sexes. This differential mortality may represent a higher natural death rate of the males or a more rapid rate of destruction in the fishery. Previous investigations have uncovered evidence for both types of differential mortality as a cause of shifting sex ratios. A greater natural death rate for males was considered by Hile (1936) to account for the decrease in the percentage of fish of that sex with increase in age in four cisco populations not subjected to a fishery.

The same author (1941) concluded that a similar change with age in the sex ratio in a stock of rock bass (*Ambloplites rupestris*) also was caused by a relatively high mortality rate for males. On the other hand, Van Oosten demonstrated that selective destruction of the sexes in the commercial fishery provided an adequate explanation of the observed changes in the sex ratio with increasing age in the Lake Huron lake herring[20] (1929) and the Lake Huron whitefish (1939). A similar conclusion was reached by Jobes (MS)[21] for the Lake Erie perch.

It seems likely that in the kiyi fishery the females may suffer the relatively greater destruction at some periods and the males at others. At seasons other than the spawning period the slower growth and more slender form of the males should cause them to become subject to destruction at a later average age than females. During the spawning season, however, the percentage of males in the catch is much greater than at other periods. At that time, therefore, the destruction of males may be relatively greater than that of females. The extent to which these opposing selective actions counteract each other is not known. Consequently no conclusion can be drawn as to the effect of the selective destruction of the sexes of the kiyi in the fishery on the variation of the sex ratio with age.

### CONSERVATION OF THE KIYI

In view of the increasing importance of the kiyi in the chub fishery of Lake Michigan, it seems advisable to consider briefly the adequacy of current regulations for the protection of the species. In Lake Michigan, chubs have legal protection through regulation of the size of gill-net meshes in all states, from closed seasons in three, and theoretically from a size limit in one. The present (1946) minimum mesh sizes permitted in gill nets employed for taking chubs are 2½ inches, extension measure, in Michigan, Wisconsin, and Indiana and 2⅜ inches in Illinois. The closed seasons for chubs are: Michigan, October 15-November 20; Wisconsin, October 10-November 15; Illinois, October 14-November 10; Indiana, none. Wisconsin has a "general" size limit of 8 inches, total length, which, however is not applied to the chubs.

In all four states bordering on Lake Michigan flexible-rule measurements of gill nets as found in use are specified although not employed in Illinois and Indiana. This method of measurement in effect requires that mesh sizes be approximately ⅛ inch larger than those of corresponding specifications used in the experimental fishing for the kiyis. In other words the 2⅜-inch mesh measured by flexible rule is roughly the equivalent of the 2½-inch mesh of the experimental nets used in this study and the 2½-inch mesh corresponds to the 2⅝-inch mesh. The examination of the data of Table 6 suggests that the present minimum legal mesh sizes, if enforced, can afford considerable pro-

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[20] In this fish, contrary to the more usual situation, the males were the more plentiful at the higher ages.

[21] Jobes, Frank W. The age and growth of yellow perch, *Perca flavescens*, (Mitchill), in Lake Erie.

tection to the stocks of the relatively small kiyi. If these mesh sizes are increased further to give more adequate protection to the general chub population the fishing pressure on the kiyi will be even less.

Present closed seasons protect the kiyi during the period of most active spawning—the last half of October and early November (Hile and Deason, 1947). There is no evidence that the species is ever abundant in the shallow waters of Indiana which has no closed season.

The general minimum legal size of 8 inches in Wisconsin, even if enforced, is of no significance to the kiyis as almost none shorter than 8 inches are taken by gill nets within the commercial range of legal mesh sizes (Table 6).

The general conclusion seems warranted that the kiyi receives good protection under current regulations (if enforced) on mesh size and closed seasons and that the improvement of these regulations for the conservation of the chubs as a group will give the species even greater protection. It is not to be inferred, of course, that these safeguards make depletion of the kiyi impossible. An unreasonably intensive fishery can do grievous harm to a stock even under regulations that would ordinarily be considered adequate.

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